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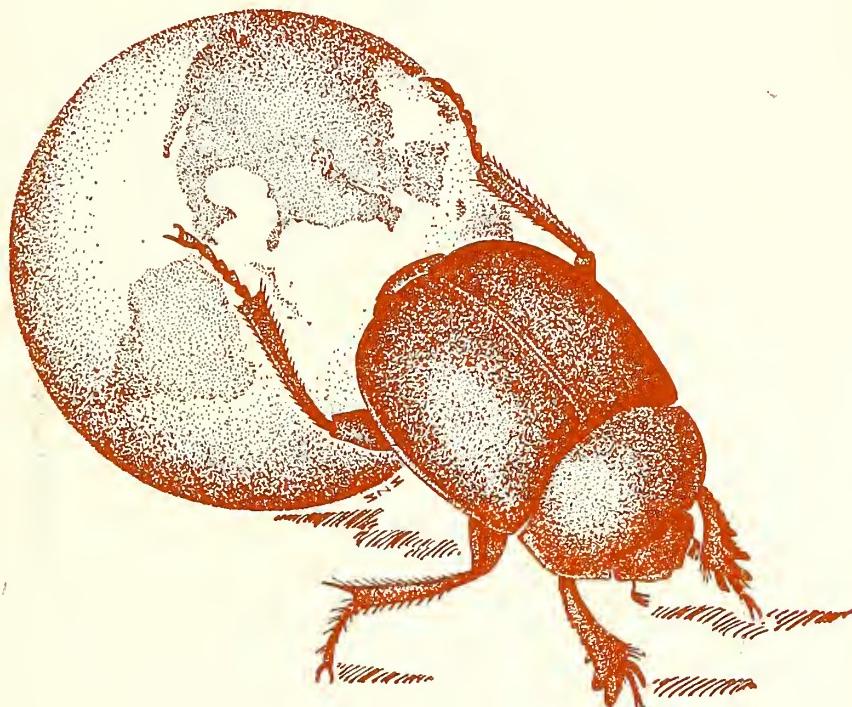
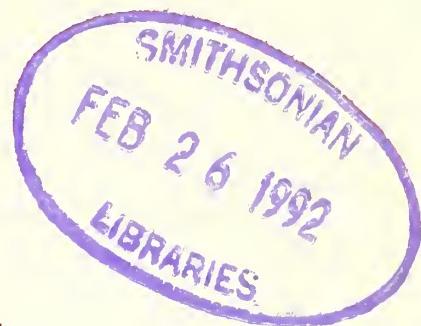
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KEY AND DIAGNOSES FOR THE GENERA OF OCHLERINI  
(HEMIPTERA: PENTATOMIDAE: DISCOCEPHALINAE)

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**Abstract.**—A key and diagnoses for 28 genera of Ochlerini are provided. New genera proposed are: *Barola*, *Catulona*, *Clypona*, *Coranda*, *Cromata*, *Forstona*, *Pseudodoxoplatys*, *Stalius* and *Uvaldus*. New species are *Barola farfala*, *Catulona pensa*, *Catulona apaga*, *Clypona aerata*, *Coranda castana*, *Cromata ornata*, *Forstona speciosa*, *Pseudodoxoplatys mendacis*, *Schaefferella fusca*, *Stalius trisinuatus* and *Uvaldus concolor*. New synonymy recognized is *Melanodermus* Stål, 1867, as a junior synonym of *Ochlerus* Spinola, 1837, resulting in revival of the combination *Ochlerus circummaculatus* Stål, 1867, and new combinations of *Coranda picipes* (Stål, 1872) and *Stalius tartareus* (Stål, 1862). *Typhoeocoris* Breddin, 1903, is placed in the synonymy of *Caracia* Stål, 1872, and *T. fulvifemur* Breddin, 1903, in the synonymy of *C. sexdens* Stål, 1872. The holotype of *Parochlerus latus* Breddin, 1904, is redescribed. The male genitalia of this species are described since only the female was known previously. A redescription of *Tetraochlerus fissiceps* Breddin, 1904, is given, and a voucher specimen is designated inasmuch as type material of this species is unknown. A lectotype and paralectotype are designated for *Ochlerus tartareus* Stål, 1862.

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The previously established genera that are considered here were formerly included in Halyini of the nominate pentatomid subfamily. A decade ago, these genera were removed to Discocephalinae (Rolston and McDonald, 1979), and subsequently Ochlerini was proposed to contain them apart from other genera in Discocephalinae (Rolston, 1981).

Members of Ochlerini are exceedingly dull in appearance, being largely of funereal hues. They have attracted little attention from taxonomists and as a consequence their classification is rudimentary. The ochlerines reside in the tropics and subtropics of the Western Hemisphere. Species of a few genera feed on herbaceous plants and are commonly collected. However, most species apparently inhabit the forest canopy, which explains their scarcity in collections and why most specimens were taken at lights or on freshly felled trees.

#### CHARACTERS INVOLVING THE ROSTRUM AND EYES

The position of the rostrum and eyes relative to each other and to other morphological features are used extensively in the key and diagnoses. The anterior limit (origin) of the labium has been determined with the venter of the insect uppermost and the longitudinal axis of the thorax and abdomen at right angles to the line of observation. The apparent relationship of the labium and eyes is altered when the head is in an abnormal position. Likewise, the relationship of the apex of the rostrum

to the abdominal sternites and of the apex of the rostral segments to the coxae is changed if the head is abnormally deflexed, reflexed or protruded. The proximity of the eyes to the pronotum is, of course, decreased in the latter case. In using these characters care must be exercised to ascertain that the head of the specimen is normally positioned.

#### MEASUREMENTS

All measurements are in millimeters and, unless qualified, are rounded to the nearest 0.05 mm. Dimensional lines on illustrations equal 0.5 mm.

#### EXCLUDED GENERA

Breddin (1903a) described *Typhoeocoris fulvifemur* as a new genus and new species from Ecuador, indicating neither the disposition of the specimen upon which he based his descriptions nor the classification other than "Rhynchoten." Froeschner (1981) ventured to catalog this insect as a halyine, but Breddin's descriptions fit a rather bizarre pentatomine described earlier by Stål (1872). I therefore propose the following synonymy:

*Caracia* Stål, 1872:14–15.

*Typhoeocoris* Breddin, 1903a:122. **NEW SYNONYMY.**

*Caracia sexdens* Stål, 1872:15.

*Typhoeocoris fulvifemur* Breddin, 1903a:122–123. **NEW SYNONYMY.**

Breddin (1912) also described from Peru a new genus and new species, *Melambrysus hoplita*, that he placed near *Ochlerus* and *Melanodermus*. Again, the disposition of the type was not revealed. From the description, *Melambrysus* seems similar to *Moncus* Stål, but for the present it must remain a *nomen dubium*.

Spinola (1850a) proposed the generic name *Audinetella* in his synoptic table, parenthetically stating that the genus was based on an unpublished species from Brazil. Description of the genus and species, *Audinetella bipunctata* Spinola, appeared the same year (Spinola, 1850b). Here, however, the two female syntypes are said to have come from Cayenne, and this is probably correct. These specimens pose a nomenclatural problem because one is *Lincus croupius* Rolston, 1983, and the other a *Paralincus* species that is apparently unnamed. *Audinetella* Spinola, 1850, is senior to both *Lincus* Stål, 1867, and *Paralincus* Distant, 1911. Use of *Audinetella* as the senior synonym of *Paralincus* would be of small consequence since there is scant primary literature on this little known genus and its junior synonym *Vauriana* Ruckes, 1958, but use of *Audinetella* as the senior synonym of *Lincus* would be very disruptive. There is considerable primary literature on this large genus, much of it concerning the role of *Lincus* species as vectors of diseases afflicting palms. Unfortunately, the description of *Audinetella bipunctata* fits only *Lincus croupius* in several critical aspects, so there is actually no choice in associating the binomen and specimen. For these reasons I am petitioning the International Commission on Zoological Nomenclature to suppress the binomen *Audinetella bipunctata* Spinola, 1850, for purposes of priority.

### Ochlerini Rolston, 1981

*Diagnosis.* Superior surface of third tarsal segment of hind legs shallowly excavated in females (only flattened in *Adoxoplatys*) and sometimes in males.

Trichobothria on at least last sternite located laterad of adjacent spiracles, excepting *Pseudodoxoplatys* with mesial trichobothrium of each pair on last sternite on imaginary line tangential to, and projecting caudad from, spiracular openings on last two sternites (Fig. 5). Basal segment of rostrum projecting caudad of bucculae, terminating on prosternum. Mesosternum thinly carinate mesially, metasternum usually so. Metapleural ostioles each accompanied by auricle, this sometimes elongated but not drawn out into ruga. Scutellum longer than wide at base (excepting brachypterous forms). All tibiae broadly sulcate. Spiracles present on paratergite 8 of females, on sternite 8 of males.

Labium usually arising on or posterior to plane transecting head at right angles to longitudinal axis of body and at anterior limit of eyes, but arising before this plane in several genera (*Adoxoplatys*, *Neodoxoplatys*, *Pseudodoxoplatys*; *Ochlerus*, *Orbatina*, *Schraderia*; and *Phereclus*).

*Comments.* Only the tarsal character appears unique among western hemisphere pentatomids, all other characteristics of the tribe appearing in various combinations elsewhere. The tribe's greatest affinity outside of the subfamily is with Pentatomini.

#### KEY TO GENERA OF OCHLERINI

- |       |  |  |
|-------|--|--|
| 1.    | Hemelytra fully developed .....  | 2  |
| -     | Brachypterous, membranes of hemelytra much reduced or absent .....   | 32   |
| 2(1). | Clearly defined intercalary segment present at base of 2nd rostral segment; metasternum broadly sulcate between lateral rims, with or without median, longitudinal carina in sulcus .....  | 3  |
| --    | Intercalary rostral segment absent; metasternum usually without lateral rims, usually carinate; flat or tectiform if lateral rims present .....  | 4  |
| 3(2). | Antennae 4-segmented; inferior surface of femora armed with many small tubercles of similar size, most of them in 2 rows .....   | <i>Adoxoplatys</i> Breddin (p. 6)          |
| -     | Antennae 5-segmented; inferior surface of femora armed with preapical pair of spines, of which at least mesial member is stout, and usually with lesser spines or tubercles .....  | <i>Neodoxoplatys</i> Kormilev (p. 6)       |
| 4(2). | Both trichobothria of each pair on sternite 7 laterad of imaginary line tangential to outer margin of spiracular openings on sternites 6 and 7 and projecting caudad (Fig. 9); length of head before ocelli usually less than 0.8 of width of head across eyes; sides of abdomen usually convex from dorsal view ..... | 5  |
| -     | Mesial trichobothrium of each pair on sternite 7 on such imaginary line (Fig. 5); length of head before ocelli 0.8 or more of width of head across eyes; sides of abdomen subparallel (Fig. 4) .....   | <i>Pseudodoxoplatys</i> , new genus (p. 7) |
| 5(4). | Width of scutellum at distal ends of frena about 0.6 or more of basal width; costal angles of coria projecting little if any past apex of scutellum .....  | 6  |
| -     | Width of scutellum at distal ends of frena less than 0.6 of basal width; costal angles of coria projecting well beyond apex of scutellum .....   | 10   |
| 6(5). | Scutellum reaching apex of abdomen .....   | <i>Moncus</i> Stål (p. 8)                  |
| -     | Scutellum shorter, an imaginary, transverse line at apex of scutellum crossing penultimate connexival sclerites .....  | 7  |

- 7(6). Anteapical tooth present on lateral margins of each jugum (Fig. 6) ..... *Schraderia* Ruckes (p. 9)  
   — Lateral margins of juga unarmed ..... 8
- 8(7). Humeral angles subacute, produced laterad of hemelytra by distance subequal to one-half width of eye; elevated edge of each evaporative area sigmoid (Fig. 8) ...  
   — Humeral angles little produced; elevated edge of each evaporative area usually arcuate (Fig. 10) ..... 9
- 9(8). Anterolateral angles of pronotum projecting anteriorly little if any beyond posterior limit of eyes (Fig. 11); scutellum not constricted near posterior ends of frena; metasternum with thin, weak carina ..... *Ochlerus* Spinola (p. 10)  
   — Anterolateral angles of pronotum projecting anteriorly well past posterior limit of eyes, reaching near middle of eyes; scutellum usually slightly constricted near posterior ends of frena; mestasternum flat, or tectiform, or thinly and weakly carinate ..... *Stalius*, new genus (p. 11)
- 10(5). Space between each eye and pronotum equal to or greater than 0.2 diameter of eye (Figs. 21–24) ..... 11  
   — Eyes contiguous with pronotum or nearly so ..... 15
- 11(10). Labium arising before imaginary plane bisecting head at anterior limit of eyes ..... *Phereclus* Stål (p. 14)  
   — Labium arising behind such a plane ..... 12
- 12(11). Inferior surface of femora armed distally with small, peg-like tubercles, these reduced or absent on posterior femora ..... *Paralincus* Distant (p. 14)  
   — Inferior surface of femora smooth or granulate ..... 13
- 13(12). Space between each eye and pronotum greater than one-half diameter of eye (Fig. 23); juga shorter than tylus ..... *Eritrachys* Ruckes (p. 15)  
   — Space between each eye and pronotum less than one-half diameter of eye (Figs. 24, 25); juga as long as or longer than tylus ..... 14
- 14(13). Second rostral segment attaining mesocoxae, rostral apex lying on sternite 3 ..... *Herrichella* Distant (p. 15)  
   — Second rostral segment attaining metacoxae, rostral apex lying on sternite 6 ..... *Barola*, new genus (p. 16)
- 15(10). Second rostral segment terminating between procoxae and mesocoxae; rostrum not projecting beyond sternite 3, usually not reaching onto abdomen ..... 16  
   — Second rostral segment attaining anterior limit of mesocoxae, or nearly so, or reaching beyond this point; rostrum extending onto or beyond sternite 3 ..... 19
- 16(15). Anterolateral margins of pronotum convex; juga separated before tylus, pincer-shaped (Fig. 29) ..... *Clypona*, new genus (p. 17)  
   — Anterolateral margins of pronotum concave or sinuous; juga contiguous before tylus or nearly so ..... 17
- 17(16). Anterolateral margins of pronotum slightly sinuous with small, triangular tooth at anterolateral angles ..... 18  
   — Anterolateral margins of pronotum concave with anterolateral angles projecting forward to anterior limit of eyes, this projection curving mesad and dorsad ..... *Forstona*, new genus (p. 20)
- 18(17). Basal plates somewhat tumescent near posterior margin, unevenly convex in profile; pygophore strongly concave mesially ventrad of posterior margin; antennae 4-segmented ..... *Miopygium* Breddin (part) (p. 19)  
   — Basal plates evenly convex; pygophore convex mesially ventrad of posterior margin; antennae 5-segmented ..... *Uvaldus*, new genus (part) (p. 25)
- 19(15). Humeri strongly emarginated (Fig. 35); veins of hemelytral membranes sometimes reticulated ..... *Schaefferella* Spinola (part) (p. 21)

- Humeri weakly or not emarginated; veins of hemelytral membranes simple or furcate, often with some basal cells ..... 20
- 20(19). Anteocular processes well developed, acute (Figs. 43, 44, 47) ..... 21
  - Anteocular margins of head projecting at most as obtuse processes ..... 23
- 21(20). Pronotum scarcely declivitous, anterolateral angles broadly rounded (Fig. 43) ....  
..... *Alathetus* Dallas (part) (p. 23)
- Pronotum decidedly declivitous, anterolateral angles narrowly rounded or angular ..... 22
- 22(21). Disk of basal plates swollen near posterior margin (Fig. 45); pygophore about one-fourth as wide as maximum width of abdomen, posterior surface lacking subconical projection ..... *Alitocoris* Sailer (part) (p. 23)
- Disk of basal plates almost evenly convex; pygophore about two-fifths as wide as maximum width of abdomen, bearing large subconical projection on posterior surface ..... *Macropygium* Spinola (p. 24)
- 23(20). Second rostral segment ending between mesocoxae, rostral apex of female and usually of male not reaching sternite 6 ..... 24
- Second rostral segment projecting past mesocoxae, rostral apex of both sexes extending to or beyond sternite 6 ..... 29
- 24(23). Disk of basal plates swollen near posterior margin, or their posterior margin standing well out from 9th paratergites, these profoundly concave basally, forming pit; third antennal segment at least twice length of second ..... 25
- Disk of basal plates not conspicuously swollen, their posterior margin appressed to 9th paratergites; length of third antennal segment much less than twice length of second ..... 26
- 25(24). Basal plates evenly convex, their posterior margin standing well out from 9th paratergites (Fig. 53); 9th paratergites profoundly concave at base, each together with adjacent margin of basal plate forming pit; dorsal margin of pygophore projecting at bottom of mesial emargination as nearly horizontal projection ...  
..... *Uvaldus*, new genus (part) (p. 25)
- Disk of basal plates with swollen area, posterior margin appressed to 9th paratergites, these not forming basal pit; pygophore without projection at base of emargination ..... *Alitocoris* Sailer (part) (p. 23)
- 26(24). Lateral margins of juga anterior to anteocular concavity tapering sharply toward apex (Fig. 65) ..... 27
- Lateral margins of juga parallel or subparallel between anteocular concavity and apex ..... 28
- 27(26). Antennae 5-segmented ..... *Parochlerus* Breddin (p. 27)
  - Antennae 4-segmented ..... *Tetrochlerus* Breddin (p. 29)
- 28(26). Second gonocoxae visible (Figs. 36, 39); humeri noticeably emarginated, produced laterad of base of hemelytra by about two-fifths width of eye (Fig. 35) ....  
..... *Schafferella* Spinola (part) (p. 21)
- Second gonocoxae hidden (Figs. 72, 78); humeri not produced ..... *Catulona*, new genus (p. 30)
- 29(23). Length of second antennal segment less than one-third length of third antennal segment and less than width of eye ..... *Alitocoris* Sailer (part) (p. 23)
  - Second antennal segment at least one-half as long as third antennal segment and longer than width of eye ..... 30
- 30(29). Metasternum flat or slightly tectiform, sometimes weakly carinate for part of its length ..... *Lincus* Stål (p. 35)
  - Metasternum clearly carinate mesially for entire length ..... 31

- 31(30). Juga exceeding tylus, their lateral margins briefly subparallel between anteocular concavity and apex (Fig. 79) ..... *Cromata*, new genus (p. 33)  
 - Tylus exceeding juga; lateral margins of juga before anteocular concavity tapering toward apex (Figs. 84, 86) ..... *Coranda*, new genus (p. 36)
- 32(1). Pronotum strongly explanate (Fig. 43) ..... *Alathetus* Dallas (part) (p. 23)  
 - Pronotum not explanate or with only anterolateral angles strongly produced .... 33
- 33(32). Anterolateral angles of pronotum extending anteriorly well beyond eyes; hemelytral membranes lacking ..... *Brachelytron* Ruckes (p. 38)  
 - Anterolateral angles of pronotum not projecting anteriorly beyond eyes; hemelytral membrane present but much reduced ..... *Miopygium* Breddin (part) (p. 19)

*Adoxoplatys* Breddin, 1903

*Adoxoplatys* Breddin, 1903b:368; Kirkaldy, 1909:XXXIII, 238 (type species designated); Kormilev, 1949:315–316, 324 (description, species keyed); Kormilev, 1950: 343 (synonymy); Kormilev, 1955:12–15 (Breddin's species redescribed, species keyed); Ruckes, 1958:23 (systematic position). (Type species *Adoxoplatys minax* Breddin, 1903, by subsequent designation, Kirkaldy, 1909.)

**Diagnosis.** Mesial tubercle at base of abdominal venter broad, flat, apposed by sulcate metasternum. At least anterior femora armed on inferior surface with 2 irregular rows of small tubercles; superior surface of third tarsal segment of hind legs flattened but not excavated. Labium arising well before imaginary plane bisecting head at anterior limit of eyes; second rostral segment usually attaining mesocoxae, with well defined intercalary segment at base; apex of rostrum usually on or beyond sternite 5. Length of head before ocelli 0.6–0.8 of width across eyes. Antennae 4-segmented. Juga surpassing tylus. Width of scutellum at distal end of frena nearly one-half of basal width. Coria extending well past apex of scutellum. Body depressed.

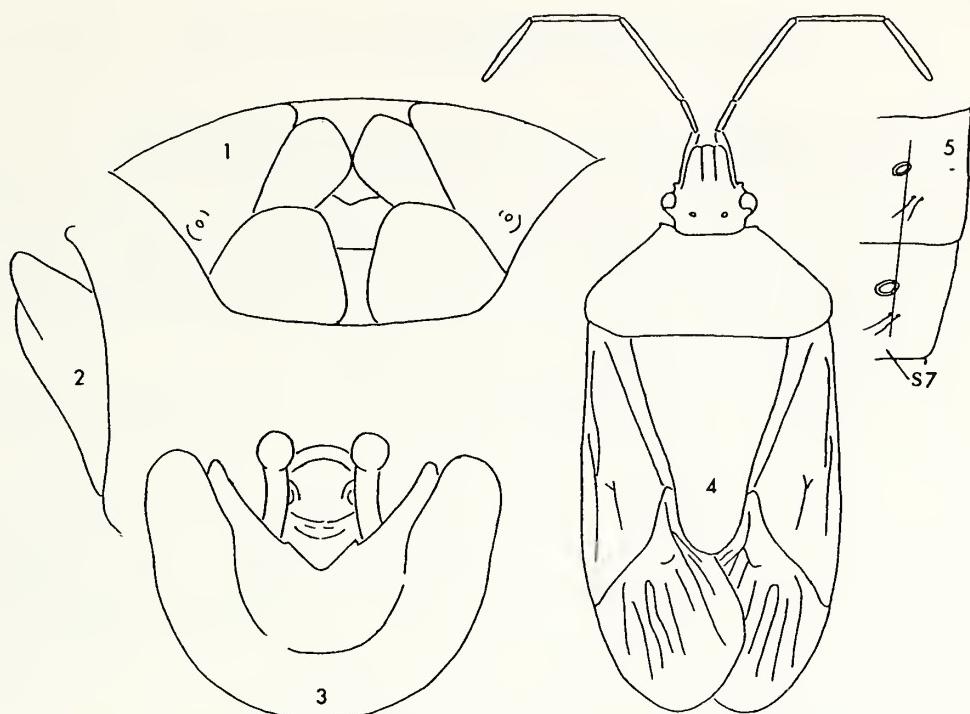
**Comments.** This genus and *Neoadoxoplatys* are unusual among ochlerines in having a sulcate metasternum, a prominent intercalary rostral segment, and usually a flattened rather than excavated superior surface of the third tarsal segment of the hind legs in both sexes.

The genus ranges from Panama to Argentina and contains 8 nominal species.

*Neoadoxoplatys* Kormilev, 1956

*Neoadoxoplatys* Kormilev, 1956:4; Ruckes, 1958:23 (systematic position). (Type species *Neoadoxoplatys saileri* Kormilev, 1956, by original designation.)

**Diagnosis.** Metasternum broadly and shallowly sulcate, without median carina but sometimes tectiform. Inferior surface of each femur armed with one or two pairs of preapical spines, some spines stout and conspicuous; superior surface of third tarsal segment of hind legs flattened in females, sometimes excavated. Base of abdominal venter unarmed. Labium arising before imaginary plane bisecting head at anterior limit of eyes; second rostral segment reaching mesocoxae, with intercalary segment at base; apex of rostrum on or beyond sternite 5. Antennae 5-segmented. Juga longer than or subequal to tylus. Length of head before ocelli 0.7 of width across eyes. Width



Figs. 1–5. *Pseudadoxoplatys mendacis*. 1. Genital plates, caudoventral view. 2. Pygophore, lateral view. 3. Pygophore, caudal view. 4. Habitus, with hemelytra slightly open. 5. Spiracles and trichobothria on left side of sternites 6 and 7. Symbol: sternite 7 (S7).

of scutellum at distal end of frena 0.4–0.5 of basal width. Coria projecting far past apex of scutellum. Body depressed.

*Comments.* The genus ranges from Mexico to Argentina and contains 3 nominate species.

#### ***Pseudadoxoplatys*, new genus**

Figs. 1–5

Type species *Pseudadoxoplatys mendacis*, new species.

*Diagnosis.* Mesial trichobothrium of pair on each side of sternite 7 located on line tangential to lateral margin of spiracular openings on sternites 6 and 7 and projected posteriorly (Fig. 5). Length of head before ocelli 0.8 of width across eyes. Metasternum flat with thin, weak, mesial carina. Base of abdomen and femora unarmed. Labium arising before an imaginary plane bisecting head at anterior limit of eyes, even before antennifers; second rostral segment reaching mesocoxae; apex of rostrum on sternite 5. Antennae 5-segmented; basal segment projecting well beyond apex of head. Width of reticulated part of one eye 0.2 width of head across eyes. Juga and tylus subequal in length. Width of scutellum at distal end of frena about one-half of basal width; costal angles of coria surpassing apex of scutellum. Sides of abdomen subparallel.

*Comments.* This genus bears a strong resemblance to *Adoxoplatys* and *Neoadoxoplatys* because of the body shape (Fig. 4). However, it is unlike *Adoxoplatys* or *Neoadoxoplatys* in having unarmed femora, in lacking an intercalary rostral segment and in having the metasternum asulcate.

The excavated superior surface of the third tarsal segment of the hind legs of females places this genus among the ochlerines.

**Pseudadoxoplatus mendacis, new species**  
Figs. 1–5

*Description.* Dark castaneous to fuscous with no pale markings.

Head 3.0–3.2 wide across eyes, 2.9–3.3 long. Width of eyes 0.6–0.7, interocular width 1.7–2.0. Distance between ocelli 0.7–0.8, across ocelli 1.15–1.3. Head almost rectangular, scarcely concave before eyes; lateral margins of juga narrowly reflexed. Segments I–V of antennae 1.6–1.8, 0.7–1.0, 2.9–3.4, 2.5–2.8, 2.4–2.7 in length. Segments II–IV of labium 2.6–2.9, 2.4–2.9, 2.3–2.7 long.

Pronotum 6.9–7.8 wide at humeri, 3.0–3.3 long mesially. Anterolateral margins nearly straight; anterolateral angles obsoletely toothed; humeri not produced, rounded (Fig. 4).

Scutellum 4.5–5.4 wide at base, 5.7–6.5 long, without fovea in basal angles; frena extending about two-thirds of distance from base to apex. Costal angles of coria above penultimate tergum, far surpassing apex of scutellum; membranes fumose, each with about 8 simple or furcate veins. Connexiva moderately exposed, with lighter colored marginal spot in middle of each segment.

Metasternal carina thin, becoming evanescent posteriorly.

Genital plates as in Figure 1. Emargination in posterior pygophoral margin deep, U-shaped from caudal view (Fig. 3). Dorsal margin of inferior ridge V-shaped. Posterior corners of pygophore incised, apparently at junction of lateral pygophoral walls and inferior ridge. Parameres visible from caudal view, their apices enlarged, ovoid. Posterior pygophoral margin sigmoid in profile (Fig. 2).

Body length 15.2–17.3.

*Types.* Holotype, ♂ labeled “PERU: Madre de Dios, Rio Tambopata Reserve, 30 km SW of Puerto Maldonado, 290 m, Nov. 1–26, 1982, Edward S. Ross.” Deposited in the California Academy of Sciences.

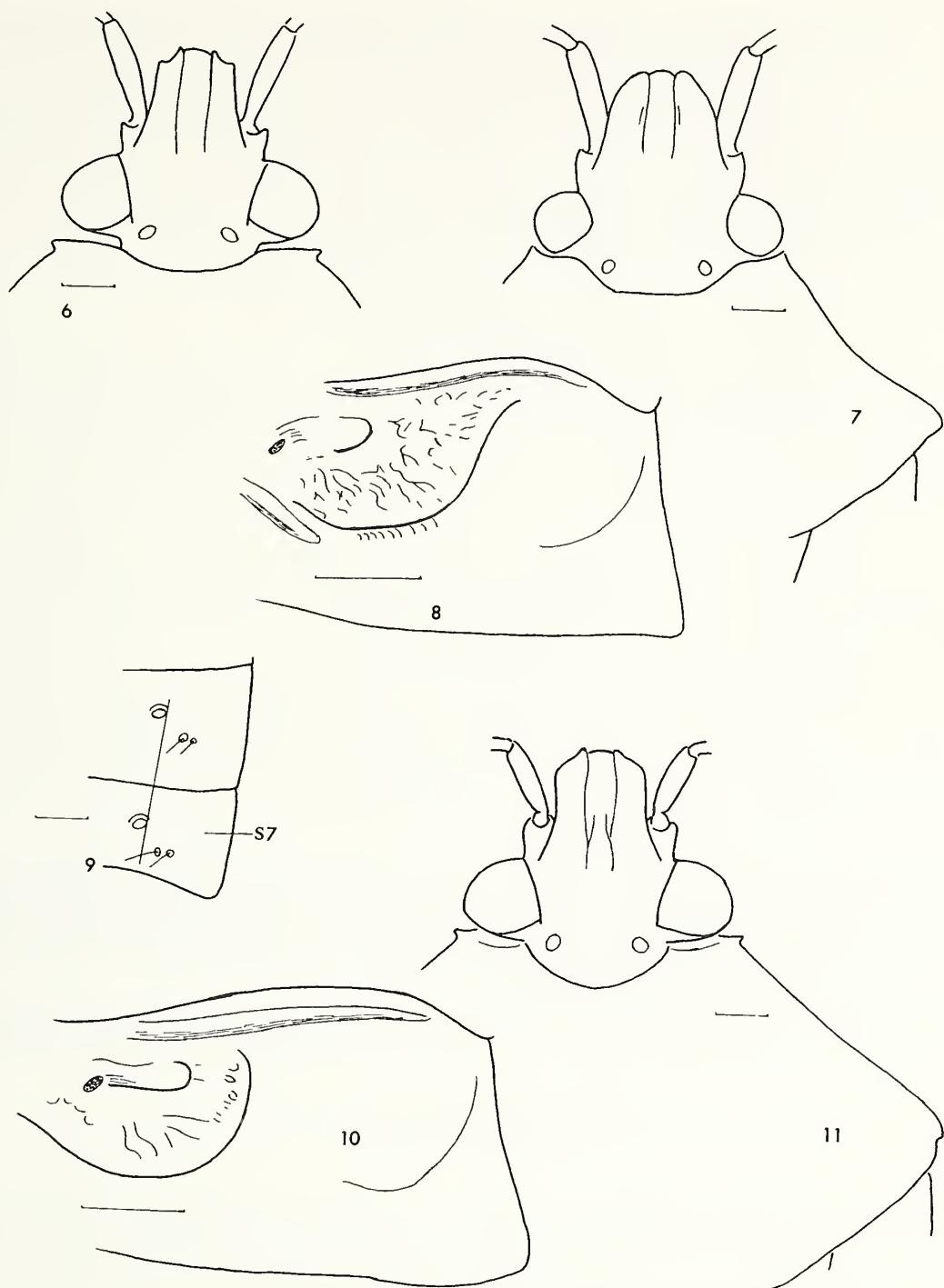
Paratypes, 4♀. 1♀ labeled same as holotype (LHR); 1♀ labeled “Frans Steinback Coll. 1956. Todos Santos Prov. Chaparo Dep. 500 M. Cochabamba, Bolivia.” and “J. C. Lutz Collection. 1961.” (NMNH); 1♀ labeled “Bolivia: Dept. of Santa Cruz, 1120 ft. elevation” and “R. B. Cumming 12-X-59 black light trap” (RMB); and 1♀ labeled “Bolivia: Saavedra, Dept. Santa Cruz Agr. Exp. Sta.” and “R. B. Cumming. 27-XII-59. Black light trap” (AMNH).

*Moncus* Stål, 1867

*Moncus* Stål, 1867:524; Stål, 1872:12, 13 (keyed); Distant, 1911:245 (synonymy).  
(Type species *Ochlerus obscurus* Dallas, 1851, by monotypy.)

*Hemingius* Distant, 1899:423–424 (synonymized by Distant, 1911). (Type species *Ochlerus scaber* Walker, 1867 [= *Ochlerus obscurus* Dallas] by monotypy.)

*Diagnosis.* Scutellum extending to apex of abdomen, 0.8 as wide at distal end of frena as at base, narrowest there, again widening before apex. Eyes large, reticulated part of each 0.3 width of head across eyes. Labium arising on imaginary plane bisecting head at anterior limit of eyes; second rostral segment reaching mesocoxae; apex of rostrum on sternite 5 or 6. Antennae 5-segmented; basal segment projecting past apex of head. Juga and tylus subequal in length, former compressed apically and pinched around tylus. Length of head before ocelli 0.6 of width across eyes.



Figs. 6–11. 6. *Schraderia hughesae*, head. 7, 8. *Orbatina fulginia*. 7. Head and part of pronotum. 8. Evaporative area, left metapleuron. 9–11. *Ochlerus handlirschi*. 9. Spiracles and trichobothria on left side of sternites 6 and 7. 10. Evaporative area, left metapleuron. 11. Head and part of pronotum. Symbol: sternite 7 (S7).

*Comments.* The size of the scutellum set this genus apart from all other ochlerines. There are 2 nominate species, both South American.

*Schraderia* Ruckes, 1959  
Fig. 6

*Schraderia* Ruckes, 1959:3–5. (Type species *Schraderia hughesae* Ruckes, 1959, by original designation.)

*Diagnosis.* Small preapical tooth present on lateral margin of each jugum (Fig. 6).

Similar to *Ochlerus* in other respects excepting male genitalia. Parameres divergent, essentially linear (stem of parameres subparallel or convergent in *Ochlerus*; head of parameres usually expanded laterad, forming right angle with stem).

*Comments.* The antepical tooth on the lateral margin of each jugum distinguishes members of *Schraderia*.

The 2 nominate species are from Central America.

*Orbatina* Ruckes, 1960

Figs. 7, 8

*Orbatina* Ruckes, 1960:228–229. (Type species *Orbatina fuligina* Ruckes, 1960, by original designation.)

*Diagnosis.* Humeral angles moderately produced laterad, right angular (Fig. 7). Width of reticulated part of one eye little more than 0.2 width of head across eyes, 0.7 of distance between ocelli. Labium arising well before imaginary plane bisecting head at anterior limit of eyes; second rostral segment reaching mesocoxae or nearly so; apex of rostrum on sternite 5. Antennae 5-segmented; first segment clearly exceeding apex of head. Juga and tylus subequal in length. Length of head before ocelli 0.75 of width across eyes. Width of scutellum at distal end of frena 0.6 of basal width. Costal angles of coria not or scarcely surpassing apex of scutellum; scutellum and coria terminating above tergum 6. Elevated margin of evaporative areas sigmoid (Fig. 8).

*Comments.* Among the ochlerine genera in which the scutellum is nearly as long as or longer than the coria, and in which the scutellar width at the end of the frena is about 0.6 or more of the basal width, *Orbatina* is distinguished by the laterally produced humeri and relatively small eyes.

This genus is monotypic and known from Colombia, Bolivia and Panama.

*Ochlerus* Spinola, 1837

Figs. 9–11

*Ochlerus* Spinola, 1837:294; Herrich-Schäffer, 1844:63–64 (description, species keyed); Dallas, 1851:150, 156–158 (keyed, synonymy, species keyed); Stål, 1867:524 (keyed); Stål, 1872:12, 13 (keyed, synonymy); Breddin, 1910:615–616 (genitalia). (Type species *Ochlerus cinctus* Spinola, 1837, by monotypy.)

*Menipha* Amyot and Serville, 1843:112 (synonymized by Stål, 1867). (Type species *Menipha brunnea* Amyot and Serville, 1843 [= *Ochlerus cinctus* Spinola, 1837], by monotypy.)

*Melanodermus* Stål, 1867:524; Stål, 1872:13. (Type species *Ochlerus circummaculatus* Stål, 1860, by subsequent designation, Kirkaldy, 1909:XXXII.) **NEW SYNONYMY.**

*Diagnosis.* Eyes large, width of reticulated part of an eye nearly 0.3 width of head across eyes, subequal to distance between ocelli (Fig. 11). Labium arising before imaginary plane bisecting head at anterior limit of eyes; second rostral segment reaching mesocoxae; apex of rostrum on sternite 5, 6 or 7. Antennae 5-segmented; basal segment projecting well beyond apex of head. Juga and tylus subequal in length; juga unarmed, subacute or obliquely truncate at apex, there narrow. Length of head

before ocelli 0.7 of width across eyes. Tooth at anterolateral angles of pronotum small, usually directed laterad. Width of scutellum at distal end of frena 0.6–0.75 of basal width; scutellum usually a little longer than coria, terminating above tergum 6 or 7. Metasternum thinly carinate mesially.

*Comments.* *Ochlerus circummaculatus* Stål, the type species selected by Kirkaldy (1909) for *Melanodermus*, differs only trivially from other *Ochlerus* species, most notably in the slightly larger tooth at the anterolateral angles of the pronotum and the longer tooth on the bucculae. *Melanodermus* therefore becomes a junior synonym of *Ochlerus*.

*Ochlerus* is one of 5 genera in which the scutellum is relatively long and broad subapically. The other genera are: *Moncus*, *Orbatina*, *Schraderia* and *Stalius*.

There are 15 nominate species in the genus. The generic range is from Mexico to Brazil.

### **Stalius, new genus**

Figs. 12–20

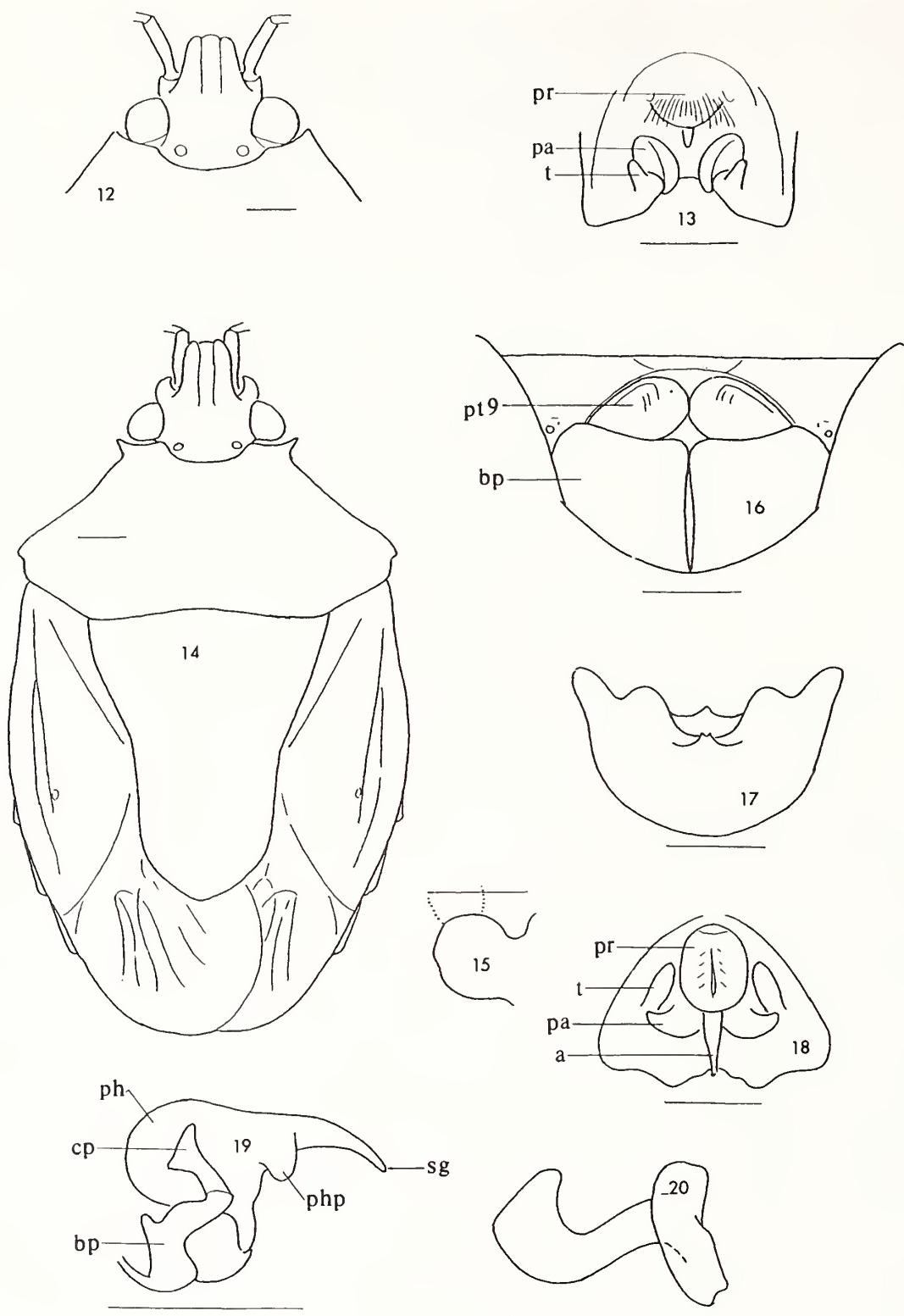
*Melanodermus* Stål, 1867:524 (in part); Stål, 1872:13 (in part).

*Stalius*, new genus. (Type species *Ochlerus tartareus* Stål, 1862.)

*Diagnosis.* Metasternum flat or tectiform, or weakly and thinly carinate mesially. Labrium arising on or near imaginary plane bisecting head at anterior limit of eyes; second rostral segment reaching metacoxae; apex of rostrum on sternites 5 or 6. Antennae 5-segmented; basal segment projecting past apex of head. Juga little or no longer than tylus, each narrowly rounded apically. Length of head before ocelli 0.6–0.7 width across eyes. Anterolateral angles of pronotum acute and directed forward, or spinose and directed anterolaterad, in either case projecting well beyond posterior limit of eyes (Figs. 12, 14). Scutellum and coria terminating above penultimate or last abdominal segment; scutellum usually a little longer than coria and slightly constricted near distal ends of frena; width of scutellum at distal ends of frena nearly 0.6 of basal width.

*Comments.* Stål (1867) originally placed two species in *Melanodermus*: *Ochlerus circummaculatus* Stål, 1860, and *Ochlerus tartareus* Stål, 1862. Kirkaldy (1909) chose *O. circummaculatus* as the type species of *Melanodermus*. I have examined the type material of these two species, which is conserved in the Naturhistoriska Riksmuseet, Stockholm. In my opinion *Ochlerus circummaculatus* belongs in the genus *Ochlerus*, which reduces *Melanodermus* Stål, 1867, to a junior synonym of *Ochlerus* Spinola, 1837. *Ochlerus tartareus* is not congeneric with *O. circummaculatus* and does not fit into any established genus. *Stalius* is therefore proposed to accommodate *O. tartareus* and the new species whose description follows. Of the 2 syntypes of *Ochlerus tartareus*, both female, the one labeled (a) "Mexico," (b) "Salle," (c) "Type," (d) "300/80," (e) "Riksmuseum Stockholm" is selected as lectotype. The paralectotype is labeled (a) "Columbia" (sic), (b) "Stål," (c) "Type," (d) "Paratypus," (e) "301/80," (f) "Riksmuseum Stockholm."

Two other species were subsequently added in *Melanodermus*: *M. picipes* Stål, 1872, and *M. dilutipes* Breddin, 1904. I have examined the holotype of *M. picipes*, also conserved in the Naturhistoriska Riksmuseet, but have been unable to locate



Figs. 12–20. 12, 13. *Stalius tartareus*. 12. Head and anterior part of pronotum. 13. Genital cup. 14–20. *Stalius trisinuatus*. 14. Habitus, composite drawing. 15. Left antennifer, lateral view. 16. Genital plates, caudoventral view. 17. Pygophore, caudal view. 18. Genital cup. 19. Aedeagus, right lateral view. 20. Right paramere, lateral view. Symbols: aedeagus (a); basal plate (bp); capitate process (cp); paramere (pa); paratergite 9 (pt9); phallotheca (ph); phallothecal process (php); prociger (pr); secondary gonopore (sg); tubercle (t).

the type of *M. dilutipes*. *M. picipes* is assigned to a new genus, *Coranda*, that is proposed later in this paper.

***Stalius trisinuatus*, new species**

Figs. 14–20

**Description.** Mostly fuscous; rostrum, legs, basal 0.2 of last antennal segment yellowish brown or at least paler than rest of antennae; distal part of coxae and numerous more or less confluent femoral spots, fuscous.

Antennifers cupped laterally about base of antennae (Figs. 14, 15). Segments I–V of antennae 0.7–0.9, 0.7–0.8, 1.2–1.4, 1.3–1.6, 1.7–1.9 in length. Width of head across eyes 2.2–2.5, length 1.7–2.0; length of head before ocelli 0.6–0.7 of width across eyes. Interocular width 1.1–1.2; distance across ocelli 0.9–1.05. Eyes slightly longer than wide; width of an eye about one-half of interocular width. Juga and tylus subequal in length; lateral margins of former subparallel between anteocular concavity and narrowly rounded jugal apices (Fig. 14). Segments II–IV of labium 2.2–2.4, 1.6–1.9, 1.8–2.1 long.

Anterolateral angles of pronotum armed with oblique spine; anterolateral margins of pronotum slightly sinuous, narrowly reflexed. Disk rough, rugose or coarsely granular. Width at humeri 5.2–6.1, mesial length 2.5–2.8.

Scutellar margin usually broadly impressed along frena; disk somewhat rugose basally, smooth caudad of frena. Width of scutellum at base 3.3–4.0, width at distal end of frena 0.6 of basal width; length 3.9–5.0. Membranes of coria darkly fumose, each with 9–10 simple veins.

Smooth, castaneous, submarginal band present on each side of abdominal venter. Area about trichobothria similarly colored.

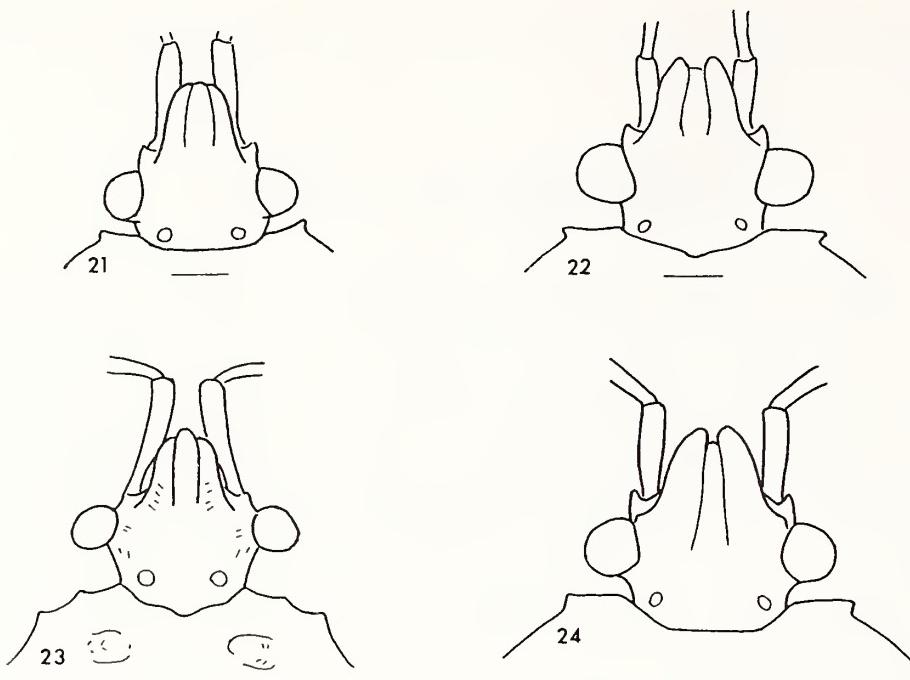
Ninth paratergite concave basally, abruptly bent in posterior direction near apex, flattened and densely setose at apex (Fig. 16). Posterior margin of basal plates shallowly concave beneath 9th paratergites from caudal view.

Posterior margin of pygophore sinuous from caudal view, broadly emarginate mesially, less deeply and less widely emarginate laterally, entire emargination consisting of 3 concave and 2 convex curves (Fig. 17). Membraneous tubercle present on each side of genital cup arising from lateral wall, well removed from posterior margin (Fig. 18). Parameres compressed, aduncate (Fig. 20). Aedeagus heavily sclerotized and pigmented, phallotheca appearing monolithic (Fig. 19).

**Types.** Holotype, ♂ labeled (a) "COSTA RICA: Puntarenas, Monteverde area. 6 June–14 June 1973. 1400–1700 meters" and (b) "Erwin & Hevel Central American Expedition, 1973." Deposited in National Museum of Natural History, Washington.

Paratypes, 2♂♂, 9♀♀. 1♂ and 5♀♀ with same labeling as holotype (2 LHR, 4 NMNH); 1♂, 2♀♀ labeled "PANAMA: Chiriquí Prov. Santa Clara. May 23–25, 1980. E. Riley & LeDoux" (1 LHR, 2 DBT); and 2♀♀ labeled "PANAMA, Chir. Renacimiento, 5000', Sta. Clara, May '80. Ratcliffe" (1 AMNH, 1 HDE).

**Comments.** The lobed antennifers, spinose pronotal lobes, and the genitalia readily distinguish this species from *S. tartareus*. The membraneous tubercles in the genital cup of *S. tartareus* are located at the posterior margin of the genital cup, and the mesial emargination in the posterior pygophoral margin is smoothly concave rather than sinuously concave (Fig. 13).



Figs. 21–24. Head and anterior margin of pronotum. 21. *Phereclus pluto*. 22. *Paralincus terminalis*. 23. *Eritrachys bituberculata*. 24. *Herrichella thoracica*.

*Phereclus* Stål, 1862

Fig. 21

*Phereclus* Stål, 1862:98; Stål, 1867:524 (keyed); Stål, 1872:14 (keyed). (Type species *Phereclus pluto* Stål, 1862, by monotypy.)

**Diagnosis.** Eyes separated from pronotum by distance equal to 0.3 diameter of an eye; width of reticulated part of one eye about one-fourth width of head across eyes. Labium arising well before imaginary plane bisecting head at anterior limit of eyes; second segment attaining mesocoxae. Anterior margin of pronotum moderately emarginated, a line drawn across anterior limit of pronotum passing along or near anterior margin of ocelli. Antennae 5-segmented; about one-half of basal segment protruding beyond apex of head; second segment about one-half as long as third. Juga subequal to tylus in length, their lateral margins tapering toward narrowly rounded apex of head (Fig. 21). Scutellum nearly 0.5 as wide at distal end of frena as at base.

**Comments.** From the other 4 ochlerine genera in which the eyes are notably separated from the pronotum, this genus may be distinguished by the origin of the labium. In *Phereclus* the labium originates well before an imaginary plane bisecting the head at the anterior limit of the eyes. In the other genera in which the eyes and pronotum are markedly separated, the labium arises behind such a plane.

The 3 nominal species of this genus come from Colombia.

*Paralincus* Distant, 1911

Fig. 22

*Paralincus* Distant, 1911:246; Rolston, 1983b:183–184 (revision). (Type species *Ochlerus terminalis* Walker, 1867, by monotypy.)

*Vauriana* Ruckes, 1958:10–12 (synonymized by Rolston, 1983b). (Type species *Vauriana bimaculata* Ruckes, 1958, by original designation.)

*Diagnosis.* Femora armed distally on inferior surface with small, peg-like, seta-bearing tubercles, these obscure or reduced in size and number on posterior femora. Eyes separated from pronotum by about one-half the diameter of an eye (Fig. 22); width of one eye about one-fourth width of head across eyes. Juga longer than tylus, convergent apically, without anteocular process or preapical tooth. Antennae 5-segmented; basal segment of each slightly surpassing apex of head. Labium arising behind imaginary plane bisecting head at anterior limit of eyes; second segment reaching mesocoxae; apex of rostrum on sternites 4–6. Length of head from anterior limit of ocelli to apex 0.7 of width across eyes. Anterior margins of pronotum shallowly concave or sinuous. Scutellar width at distal end of frena 0.5 of basal width. Costal angles of coria surpassing apex of scutellum. Metasternum carinate mesially.

*Comments.* There are 4 other genera in which the eyes are notably separated from the pronotum: *Barola*, *Eritrachys*, *Herrichella* and *Phereclus*. Of these 5 genera, only *Paralincus* has armed femora.

The 3 species of the genus are found in the Amazon basin and northern South America.

*Eritrachys* Ruckes, 1959  
Fig. 23

*Eritrachys* Ruckes, 1959:10–11. (Type species *Eritrachys bituberculata* Ruckes, 1959, by original designation.)

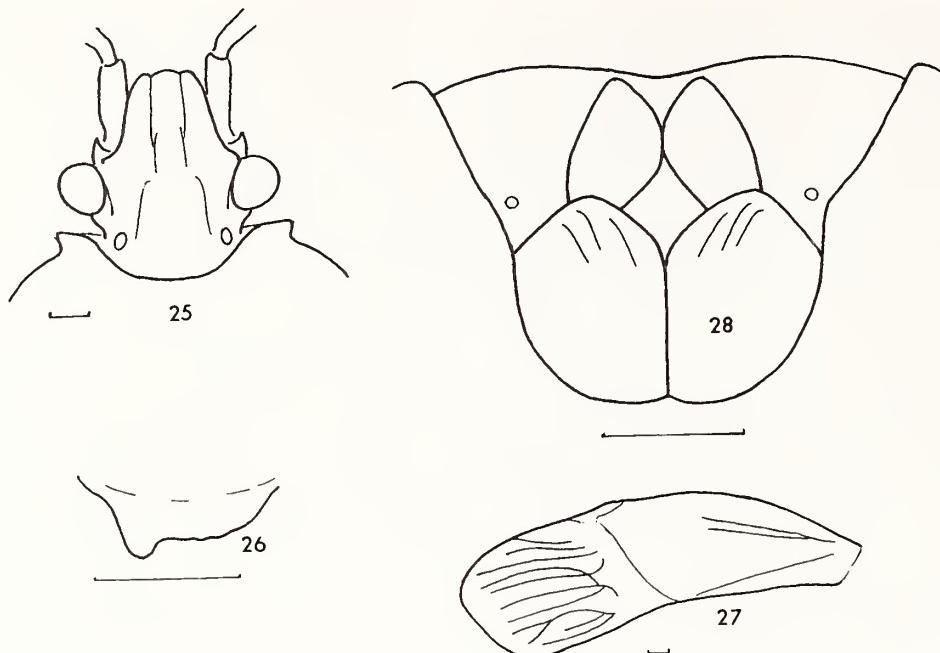
*Diagnosis.* Eyes pedunculate, separated from pronotum by a little more than one-half the diameter of an eye on anterior-posterior axis (Fig. 23). Antennae 5-segmented; first segment surpassing apex of head; second segment about half as long as third. Juga shorter than tylus. Length of head before ocelli 0.6 of width across eyes. Labium arising behind imaginary plane bisecting head at anterior limit of eyes; second rostral segment attaining mesocoxae; apex of rostrum on penultimate sternite. Pronotal emargination behind head and anterolateral margin on each side of head quite sinuous. Width of scutellum at distal end of frena 0.4 of basal width. Corium surpassing apex of scutellum. Metasternum carinate mesially.

*Comments.* The pedunculate eyes, well separated from the pronotum, are distinctive. This monotypic genus ranges from Costa Rica to Ecuador.

*Herrichella* Distant, 1911  
Fig. 24

*Herrichella* Distant, 1911:245–246. (Type species *Herrichella thoracica* Distant, 1911, by monotypy.)

*Diagnosis.* Eyes separated from pronotum by distance equal to 0.2 diameter of eye (Fig. 24). Antennae 5-segmented; first segment extending little past apex of head; length of segment II less than 0.3 that of segment III. Juga exceeding tylus. Length of head before ocelli 0.6–0.7 width across eyes. Anteocular process poorly developed, obtuse. Labium arising behind imaginary plane bisecting head at anterior limit of eyes; rostral segment II attaining anterior limit of mesocoxae; apex of rostrum reaching sternite 3. Anterior margin of pronotum moderately emarginated. Width of scu-



Figs. 25–28. *Barola farfala*. 25. Head and anterior margin of pronotum. 26. Profile of left buccula. 27. Left hemelytron. 28. Genital plates, caudoventral view.

tellum at distal end of frena 0.5 of basal width. Coria exceeding apex of scutellum. Metasternum carinate mesially.

*Comments.* The original description is misleading with respect to relationships of the rostrum to the coxae and sternites because the head of the holotype was appreciably reflexed.

This is one of 5 ochlerine genera in which the eyes and pronotum are not contiguous or nearly so. The other genera are *Barola*, *Eritrachys*, *Paralincus* and *Phereclus*. *Herrickella* differs especially from *Eritrachys* in the length of the juga relative to the tylus and in the form of the pronotum, from *Paralincus* in having unarmed femora, from *Phereclus* in the origin of the labium and from *Barola* in having a shorter rostrum, shorter second antennal segment and more developed metasternal carina.

*Herrickella* is monotypic and known only from Colombia.

#### **Barola, new genus**

Figs. 25–28

Type species *Barola farfala*, new species.

*Diagnosis.* Metasternum nearly flat, very shallowly sulcate on each side of weakly developed, broad, median carina. Labium arising behind imaginary line traversing head at anterior limit of eyes; bucculae strongly toothed (Fig. 26); segment II of rostrum reaching metacoxae, apex attaining penultimate sternite. All trichobothria well laterad of adjacent spiracle. Eyes separated from pronotum by about 0.4 maximum anterior-posterior diameter of eye (Fig. 25). Anteocular process lacking. Antennae 5-segmented; length of segment II about two-thirds that of segment III. Length of head before ocelli three-fourths of width across eyes. Anterior margin of pronotum moderately emarginate behind head, an imaginary line across anterior limits of pronotum passing near anterior limits of ocelli. Costal angles of coria surpassing apex

of scutellum, lying above penultimate connexival segment. Width of scutellum at distal end of frena about one-half of basal width. Femora unarmed.

*Comments.* This genus is similar to *Herrickella* but differs notably in having a less developed metasternal carina, a longer rostrum and differently proportioned antennal segments.

**Barola farfala**, new species  
Figs. 25–28

*Description.* Dark brown above with ivory median macule at base of scutellum and yellowish marginal macule on each connexival segment, those macules on segments 5 and 6 covering most of segment; abdominal venter brownish yellow with conspicuous dark punctuation except mesially; legs light brown with slightly darker subapical annulus on femora; last 2 antennal segments slightly lighter colored than fuscous to dark brown basal segments.

Juga not surpassing tylus at apex, their lateral margins tapering from convexity above antenniferous to apex (Fig. 25). Vertex of head sharply delineated, strongly convex, nearly tumescent. First antennal segment projecting well beyond apex of head; segments I–V of antennae 0.9, 0.6, 0.9, 2.1, 3.0 long. Segments I–IV of labium 1.5, 2.9, 2.3, 2.3 in length. Head 2.6 wide across, 2.5 long. Interocular distance 1.4; eyes 0.6 wide, 0.6–0.65 long from dorsal view; distance across ocelli 1.4. Base of antenniferous ventrally and line running from antenniferous to base of head pale.

Pronotum 6.5 wide at humeri, 2.7 long at meson. Anterolateral margins sinuous, reflexed. Punctuation rugose.

Scutellum 4.0 wide at base, 5.1 long. Apex narrowly rounded, slightly elevated on each side. Fovea in basal angles black, deeply punctured. Punctuation of disk similar to that of pronotum. Exocorium more strongly punctate than endocorium; membranes dark, each with about 11 veins; costal angle acute, submarginal (Fig. 27).

Lateral borders of prothorax broadly calloused, pale. Pleural surfaces of thorax otherwise densely punctate. Lateral borders of abdomen impunctate, shiny; sternites 3–6 with broad, impunctate sulcus; area between sulcus and lateral border uniformly and darkly punctate; spiracles oval, black.

Basal plates submarginally impressed posteriorly (Fig. 28).

Length about 14 including membranes.

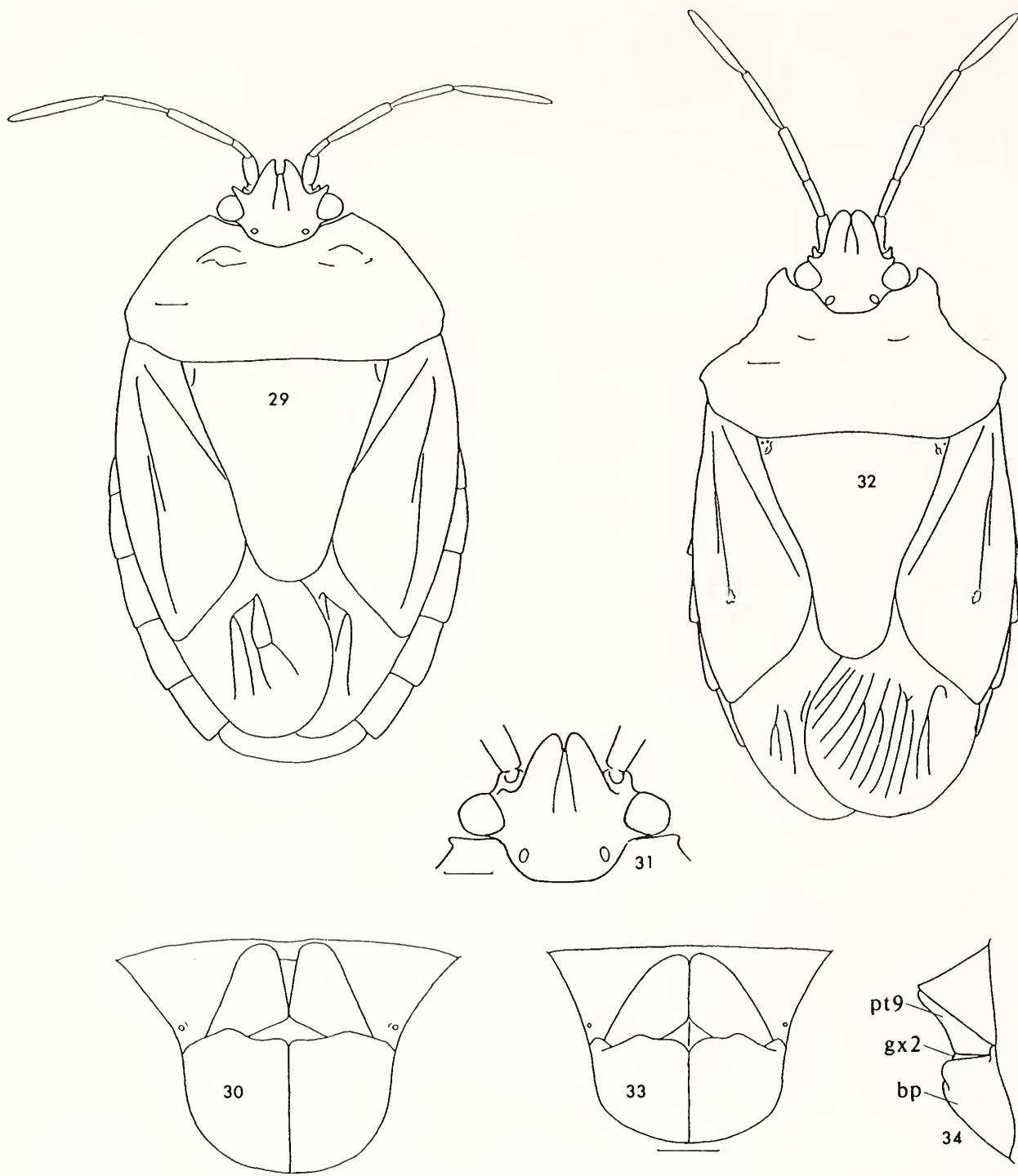
*Types.* Holotype, ♀ labeled (a) "Barro Colo. Is., Panama C.Z. VII-28-1938.," (b) "Col. by E. C. Williams, Jr." Deposited in the Field Museum of Natural History, Chicago. Segment 3 of right antenna deformed.

Paratype, 1♀ labeled "PANAMA: Prov. Chiriquí, Rovira, 5-VII-64, A. Bruce, 2500 ft. mosquito light trap" (RMB).

**Clypona**, new genus  
Figs. 29, 30

Type species *Clypona aerata*, new species.

*Diagnosis.* Second rostral segment ending between procoxae and mesocoxae; apex of rostrum lying between metacoxae; labium arising well behind imaginary plane bisecting head at anterior limit of eyes. Antennae 5-segmented; diameter of 3 basal



Figs. 29–34. 29, 30. *Clypona aerata*. 29. Habitus. 30. Genital plates, caudoventral view. 31. *Miopygium cyclopeltoides*, head and anterior pronotal margin. 32–34. *Forstona speciosa*. 32. Habitus. 33. Genital plates, caudoventral view. 34. Same, lateral view. Symbols: basal plate (bp); 2nd gonocoxae (gx2); paratergite 9 (pt9).

segments appreciably greater than that of 2 distal segments; segment II short, one-third or less length of segment III in females (males unknown). Eyes contiguous with pronotum; width of reticulated part of one eye a little less than one-fourth width of head across eyes. Anteocular process large, spinose (Fig. 29). Juga far surpassing tylus, leaving deep incision in apex of head, pincer-shaped before tylus. Length of head before ocelli 0.6 of width across eyes. Anterolateral margins of pronotum explanate; anterolateral angles obtuse. Scutellum little longer than wide at base, length 0.05

greater than basal width; width at distal end of frena 0.5 of basal width; scutellar apex above tergum 5, surpassed by costal angle of coria. Femora and base of abdomen unarmed. Metasternum thinly carinate mesially.

*Comments.* This genus differs from *Miopygium* in having 5-segmented antennae, apically dehiscent juga, a larger anteocular process and laterally explanate pronotum. It is like *Miopygium*, *Forstona* and *Uvaldus* in having a relatively short rostrum.

**Clypona aerata, new species**

Figs. 29, 30

*Description.* Dorsum fuscous to dark castaneous with scattered flecks and vermiciform lines brownish yellow, and general appearance of badly tarnished bronze. Venter colored as dorsum but more extensively pale-marked on thorax. Antennae mostly fuscous, first segment lighter toward base. Rostrum and legs brownish yellow; numerous dark spots on femora and tibiae.

Juga projecting beyond tylus by distance nearly equal to three-fourths length of tylus, narrowly rounded apically (Fig. 29); jugal margins forming incision in apex of head, first diverging then converging. Diameter of eyes 0.6; distance between ocelli 1.1. Width of head across eyes 2.7–2.8, length 2.0–2.1. Basal segment of antennae largest in diameter, segments II and III larger in diameter than segments IV and V; segments I–V of antennae 0.8, 0.5, 1.6–1.9, 1.3–1.4, 2.2–2.3 long. Bucculae obtusely angled or toothed anteriorly, percurrent caudad of angle or tooth, then curving to termination at base of head. Second through last labial segments 1.5, 0.8–0.9, 0.7–0.8 long.

Anterolateral margin of pronotum moderately convex from dorsal aspect; obtuse anterolateral angles sometimes minutely toothed; humeri somewhat bossed before junction of veins on coria; width of pronotum at humeri 6.9–7.4, length mesially 3.0–3.3. Scutellum 4.4–4.8 wide at base, 4.6–5.0 long; fovea in basal angles consisting of a few large, shallow, punctate impressions. Connexiva broadly exposed; segments forming weak serration, each with small, pale, marginal macule at middle. Membranes dark, each with about 7 veins.

Basal plates rather evenly convex; posterior margin of each sigmoid from caudal view; curving ventrad near meson, curving dorsad below 8th paratergite; posterior margin from caudoventral view concave along mesial half (Fig. 30). Length 13.0–13.5.

*Types:* Holotype, ♀, labeled "Argentina, Ledeimo, July 14–48, P. Wygodzinsky." Deposited in National Museum of Natural History, Washington.

Paratypes, 2♀♂ labeled same as holotype (1 NMNH, 1 AMNH).

***Miopygium* Breddin, 1904**

Fig. 31

*Miopygium* Breddin, 1904:153. (Type species *Miopygium cyclopeltoides* Breddin, 1904, by monotypy.)

*Diagnosis.* Rostrum relatively short, apex ranging from metacoxae onto third abdominal sternite; second segment projecting little past procoxae; labium arising well behind imaginary plane bisecting head at anterior limit of eyes. Antennae 4-seg-

mented; basal segment projecting well beyond apex of head; diameter of basal 2 segments conspicuously greater than that of last 2 segments. Anteocular process small, obtuse or acute (Fig. 31). Juga much longer than tylus, contiguous apically or nearly so. Length of head before ocelli little more than one-half width across eyes. Anterolateral margins of pronotum carinate, a short, triangular tooth present at anterolateral angles. Scutellar width at distal end of frena 0.5–0.55 of basal width; length of scutellum usually 0.1 longer than wide. Metasternum carinate mesially.

*Comments.* The rostrum of most ochlerines extends well onto the abdomen, often nearly to the abdominal apex, but in *Miopygium*, *Clypona*, *Forstona* and *Uvaldus* the rostrum does not project onto the abdomen or projects no farther than the third sternite. *Miopygium* differs strikingly from the other 3 genera of this group in having 4-segmented antennae.

There are 2 nominate species, both from Brazil. *M. cyclopeltoides* has two forms, one brachypterous.

**Forstona**, new genus

Figs. 32–34

Type species *Forstona speciosa*, new species.

*Diagnosis.* Anterolateral angles of pronotum expanded, curving around eyes, extending nearly to anterior limit of eyes (Fig. 32). Second rostral segment ending between procoxae and mesocoxae; apex of rostrum lying between metacoxae; labium arising well behind imaginary plane bisecting head at anterior limit of eyes. Antennae 5-segmented; basal segment not reaching apex of head, this segment alone of markedly greater diameter than last 2 segments; segment II three-fourths length of segment III in female (male unknown). Eyes contiguous with pronotum; width of reticulated part one-fourth width of head across eyes. Anteocular process present, acute. Juga contiguous before tylus. Length of head before ocelli 0.7 of width across eyes. Scutellar width at distal end of frena a little less than one-half basal width; length nearly 0.2 greater than basal width; apex of scutellum above tergum 5, surpassed by coastal angle of coria. Femora and base of abdomen unarmed. Metasternum thinly carinate mesially.

*Comments.* The antennae, pronotum and length of the scutellum distinguish this genus from *Miopygium*, *Clypona* and *Uvaldus*.

**Forstona speciosa**, new species

Figs. 32–34

*Description.* Dull black above and below, but with shades of yellowish brown as follows: fifth and distal part of fourth antennal segments, rostrum, tarsi, and small macule at middle of scutellar base, on disc of each corium and marginally in middle of connexival segments, the latter obscure.

Head rather flat above, densely punctate; margins before eyes narrowly reflexed, width across eyes 2.7, length 2.4. Diameter of eyes 0.6; distance between ocelli 0.9. Segments I–V of antennae 0.7, 0.8, 1.3, 1.5, 1.8 long. Bucculae subacutely toothed anteriorly, curving posteriorly to termination a little before base of head. Second through last labial segments 1.7, 1.3, 1.1 long.

Pronotum behind cicatrices and scutellum strongly rugose; coria densely punctate, weakly rugose. Pronotum 7.1 wide at humeri, 3.1 long mesially. Scutellum 4.5 wide at base, 5.0 long; fovea in basal angles not prominent, consisting of a cluster of strong punctures. Connexiva narrowly exposed. Membranes dark, each with about a dozen veins.

Basal plates tumescent submarginally along posterior margin below 9th paratergite, forming a rounded projection when viewed laterally (Figs. 33, 34).

**Type.** Holotype, ♀ labeled "Brazil, Rondonia: Vilhena, Nov. 1973. M. Alvarenga." Deposited in the American Museum of Natural History. No paratypes.

*Schaefferella* Spinola, 1850

Figs. 35–42

*Schaefferella* Spinola, 1850b:88; Spinola, 1852:128 (reprint); Stål, 1867:523 (keyed); Stål, 1872:12 (keyed, synonymy). (Type species *Schaefferella litigiosa* Spinola, 1850 [=*Cimex incisus* Herrich-Schäffer, 1839], by monotypy.)

**Diagnosis.** Humeri produced laterad of base of coria by distance subequal to one-fourth width of eye and prominently emarginated (Fig. 35). Basal 3 segments of antennae enlarged, with interspecific variation and sexual dimorphism in degree of enlargement; length of segment II ranging from less than one-half of segment III to subequal to segment III; basal segment scarcely surpassing apex of head. Anteocular process present, weak and obtuse to moderately produced (Figs. 35, 38); juga convergent or contiguous before tylus. Length of head before ocelli 0.7 of width across eyes. Labium arising behind imaginary plane bisecting head at anterior limit of eyes; segment II of rostrum reaching mesocoxae; rostrum ending on sternites 4 or 5. Width of scutellum at distal end of frena about one-half of basal width. Coria extending past apex of scutellum. Distal part of proctiger expanded laterally (Figs. 37, 40). Metasternum mesially carinate. Basal plates as in Figures 36 and 39, their disk convex with a low prominence near center.

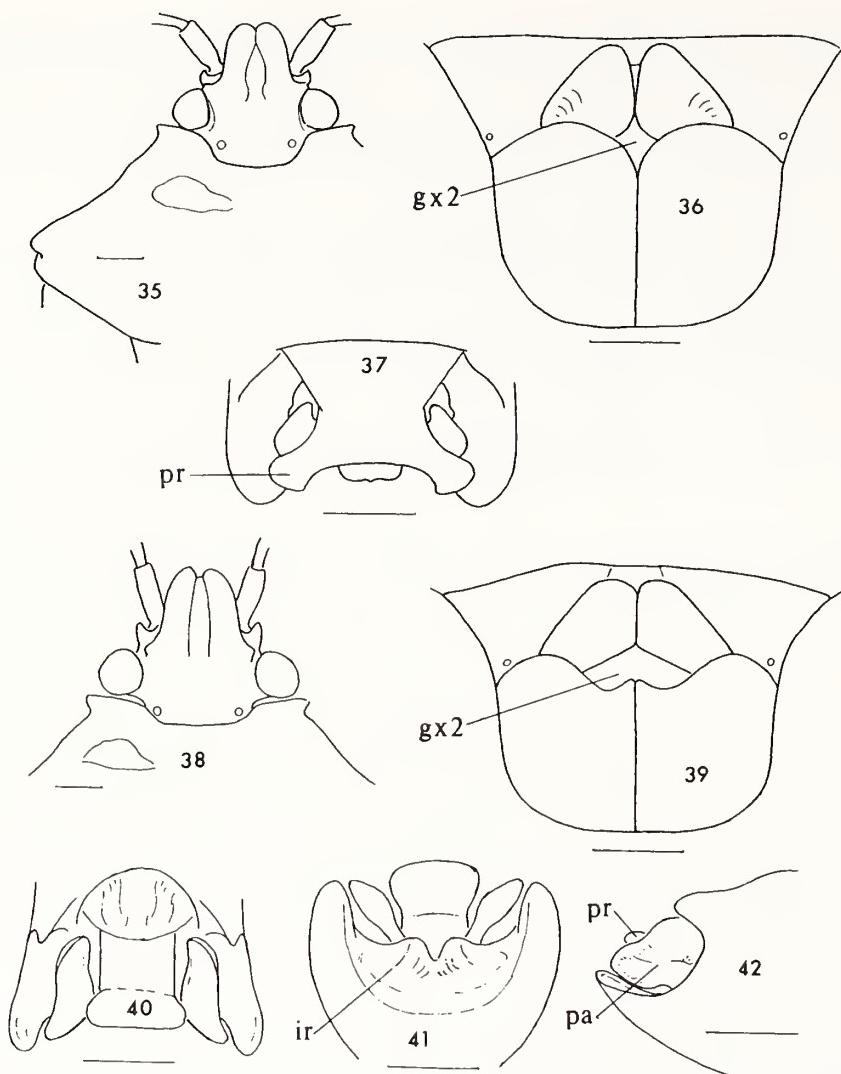
**Comment.** *Schaefferella* resembles most closely *Alitocoris* and *Macropygium* in characteristics other than those associated with the genitalia. There are two species in the genus, the type species from Brazil and the other from the Andean region.

*Schaefferella fusca*, new species

Figs. 38–42

**Description.** Fuscous with following brown to brownish yellow: basal three-tenths of last antennal segment, humeral emargination, rostrum, tarsi, and in part trochanters and coxae.

Anteocular process reduced to obtuse tubercle (Fig. 38). Juga convergent before tylus, their lateral margins subparallel between concavity before eyes and convexity at apex. Disk of head strongly punctate, vertex rugose, juga transversely rugous basally. Diameter of segments II and III of antennae (in female) only slightly greater than that of segments IV and V; segments I–V of antennae 0.9, 1.3, 1.5, 1.6, 2.0 long. Apex of rostrum reaching middle of sternite 5; length of second through last segments 2.4, 2.2, 1.8. Reticulated part of eye 0.7 wide, distance between eyes 1.6. Distance across ocelli 1.5, between ocelli 1.1. Width of head across eyes 3.1, length 2.4.



Figs. 35-42. 35-37. *Schafferella incisa*. 35. Head and pronotum. 36. Genital plates, caudoventral view. 37. Genital cup. 38-42. *Schafferella fusca*. 38. Head and anterior pronotal margin. 39. Genital plates, caudoventral view. 40. Genital cup. 41. Pygophore caudal view. 42. Distal part of pygophore, lateral view. Symbols: 2nd gonocoxae (gx2); inferior ridge (ir); paramere (pa); proctiger (pr).

Anterolateral margins of pronotum slightly sinuous; tooth at anterolateral angle flat, subtriangular. Disk rugosely punctate. Pronotal width at humeri 7.5, length at meson 3.3.

Scutellum rugose basally, finely punctured apically with a few yellowish brown dots and vermiciform marks. Basal width 4.6, length 5.2. Deep fovea present in each basal angle. Frena extending along basal six-tenths of scutellum. Veins of hemelytral membranes simple or furcate; each membrane with about 11 veins.

Genital plates as in Figure 39, with low tumescence near center of basal plates and longitudinal furrows. From caudal view, posterior pygophoral margin with deep, wide, U-shaped emargination half filled by inferior ridge (Fig. 41). Inferior ridge incised mesially, bent posterolaterad on each side of incision. Paramere compressed; posterior part of head convex on mesial face, concave on lateral face; convexities reversed on anterior part of head. Proctiger expanded distally; enlargement reflexed, concave ventrally, convex dorsally (Fig. 40). Extracting pygophore discloses in each lateral wall a large emargination framing head of parameres (Fig. 42).

*Types.* Holotype, ♂ labeled "ECUADOR. Pastaza, Cuisimi, on Rio Cuisimi, 150 km SE Puyo, 350 m. July 19–23, 1971. B. Malkin." Deposited in the American Museum of Natural History.

Paratype, ♀ labeled "PERU, Loreto. Headwaters of Loreto-Yacu, Yagua Indian Vill. April 21–May 1, 1970. B. Malkin" (LHR).

*Comment.* This species is readily distinguished from the only other known species of the genus, *S. incisa*, by the predominately fuscous color and lack of reticulation in the hemelytral membranes.

*Alathetus* Dallas, 1851

Fig. 43

*Alathetus* Dallas, 1851:160; Rolston, 1982:156. (Type species *Alathetus rufitarsus* Dallas, 1851, by monotypy.)

*Diagnosis.* Pronotum flat dorsally; anterolateral margins explanate, especially at anterolateral angles (Fig. 43). Anteocular process present. Antennae 4-segmented; basal segment reaching to or beyond apex of head. Labium arising behind imaginary plane bisecting head at anterior limit of eyes; second rostral segment attaining or surpassing mesocoxae; apex of rostrum on or beyond sternite 5. Juga surpassing tylus. In alate species length of head before ocelli 0.7 width across eyes, and width of scutellum at distal end of frena 0.4–0.5 of basal width. Metasternum carinate mesially. Brachypterous species lacking ocelli.

*Comments.* The genus contains 2 species, the type species from Jamaica and a brachypterous species, *A. haitiensis* Rolston, 1982, from Hispaniola.

The form of the pronotum in *Alathetus* is distinctive among ochlerine genera.

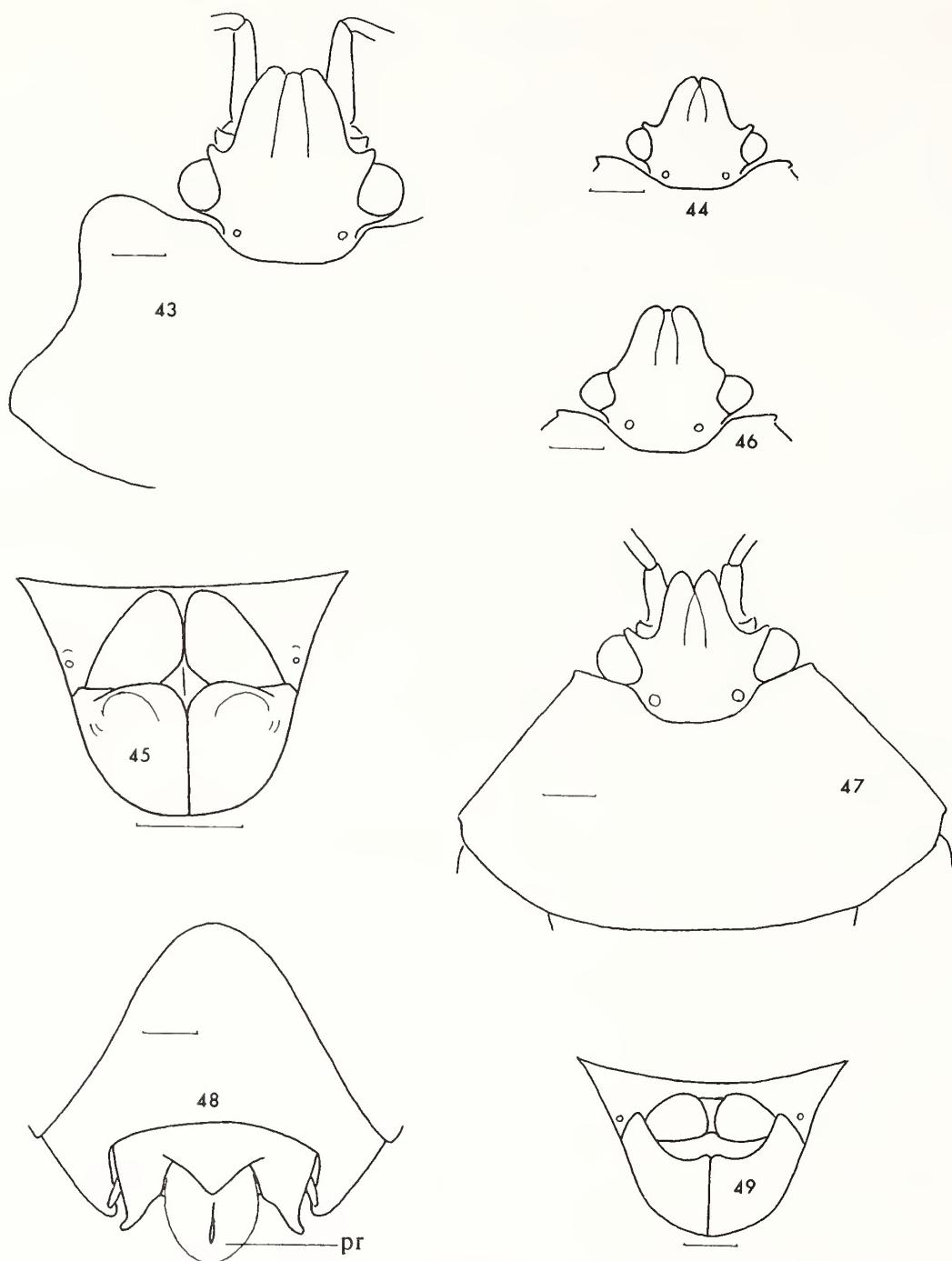
*Alitocoris* Sailer, 1950

Figs. 44–46

*Alitocoris* Sailer, 1950:69–71. (Type species *Alitocoris schraderi* Sailer, 1950, by original designation.)

*Diagnosis.* Labium arising behind imaginary plane bisecting head at anterior limit of eyes; second rostral segment nearly attaining to slightly surpassing mesocoxae; apex of rostrum reaching sternites 3–5. Length of head before ocelli 0.6–0.7 width across eyes. Anteocular process present, usually a blunt tubercle, occasionally acute and set apart by concave emargination in lateral margin of jugum (Figs. 44, 46). Antennae usually 5-segmented, 4-segmented in some species; first segment extending little or not at all beyond apex of head; basal 3 segments of 5-segmented antennae or basal 2 segments of 4-segmented antennae somewhat to much enlarged, their diameter appreciably greater than that of following segments, particularly in males of some species. Width of scutellum at distal end of frena 0.4–0.5 basal width. Coria surpassing apex of scutellum. Metasternum carinate mesially. Width of pygophore one-fourth of maximum abdominal width. Basal plates with broad tumescence near distal margin (Fig. 45). Posterior surface of pygophore concave, usually obscuring genital cup from caudal view excepting portion visible through mesial emargination.

*Comments.* There are 5 described species, all from Central America. However, undescribed species extend the genus range from Mexico to southern Brazil.



Figs. 43–49. 43. *Alathetus rufitarsis*, head and pronotum. 44, 45. *Alitocoris parvus*. 44. Head. 45. Genital plates, caudoventral view. 46. *Alitocoris manni*, head. 47–49. *Macropygium reticulare*. 47. Head and pronotum. 48. Pygophore and 7th abdominal sternite, ventral view. 49. Genital plates, caudoventral view. Symbol: proctiger (pr).

*Alitocoris* shows considerable interspecific variation with respect to size, development of anteocular processes, and antennae (relative diameter and length, and number of segments). The genitalia, however, are interspecifically similar.

*Macropygium* Spinola, 1837  
Figs. 47–79

*Macropygium* Spinola, 1837:287; Herrich-Schäffer, 1844:48 (description); Dallas, 1851:150, 158–159 (keyed, synonymy). (Type species *Macropygium atrum* Spinola, 1837 [=*Cimex reticularis* Fabricius, 1803], by monotypy.)

*Oxyrhinus* Amyot and Serville, 1843:113 (synonymized by Dallas, 1851). (Type species *Oxyrhinus subsulcatus* Amyot and Serville, 1843, by monotypy.)

**Diagnosis.** Anteocular process prominent, spinose (Fig. 47); juga convergent or contiguous apically. Basal 3 of 5 antennal segments enlarged; basal segment usually projecting beyond apex of head; segment II less than one-half length of III; segment III in males nearly twice diameter of each of last 2 segments. Length of head before ocelli 0.6 width across eyes. Labium arising behind imaginary plane bisecting head at anterior limit of eyes; second rostral segment reaching mesocoxae or nearly so; apex of rostrum on sternite 3 or 4. Anterolateral margins of pronotum explanate; anterolateral angles projecting forward to middle of eyes. Scutellar width at distal end of frena 0.5 basal width. Coria surpassing apex of scutellum. Many small tubercles scattered over inferior surfaces of femora, most prominent on front legs. Sternite 7 in male longer than all preceding sternites combined. Pygophore large, 0.4 as wide as greatest abdominal width, bearing large, mesial cone on disk (Fig. 48). Disk of basal plates rather evenly convex, without prominent, swollen area (Fig. 49).

**Comments.** This is the most frequently collected of ochlerine genera and one of the easiest to recognize. The genus is currently monotypic, although there are differences among male genitalia that suggest the possibility of one or more additional species.

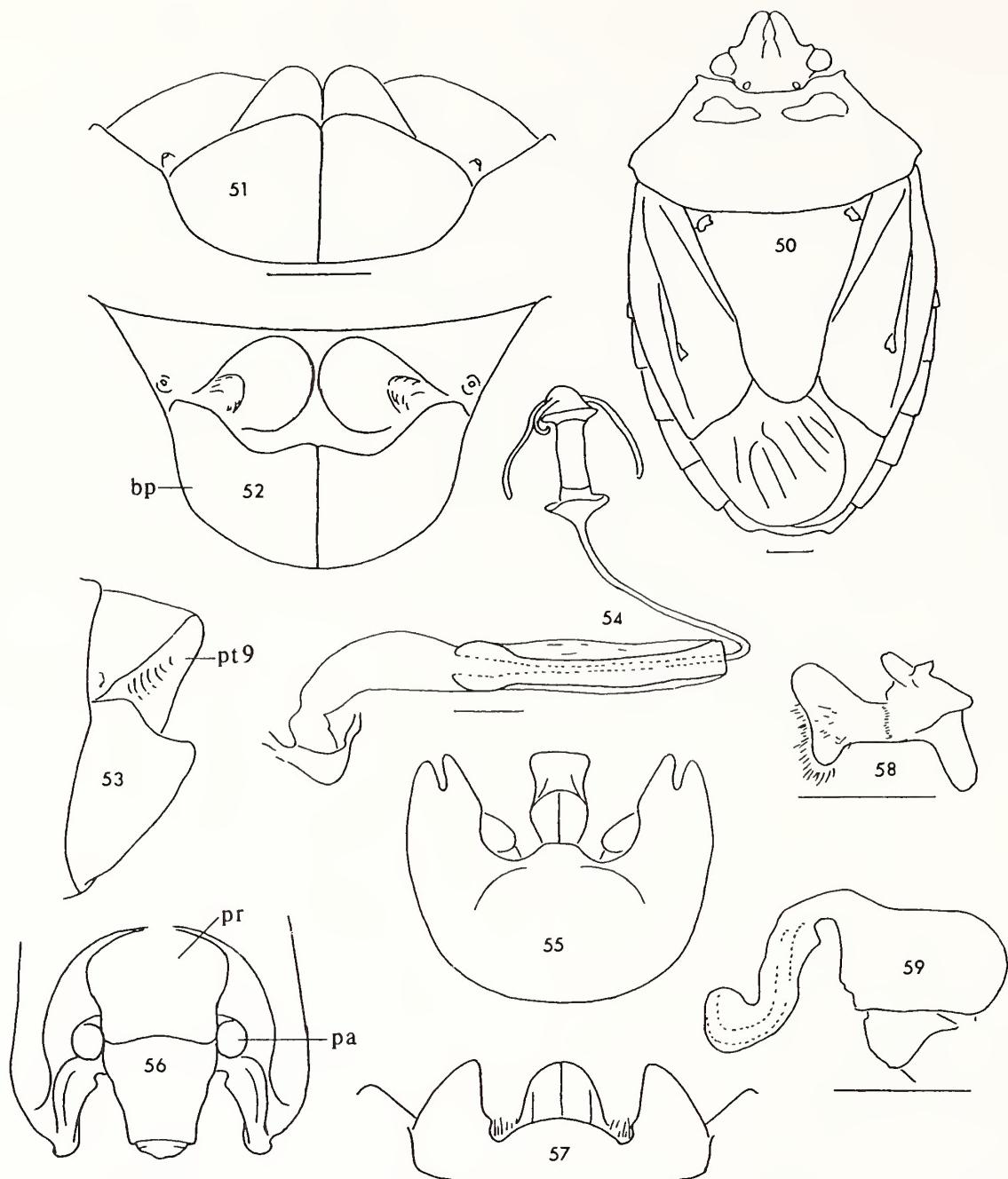
**Uvaldus, new genus**  
Figs. 50–59

Type species *Uvaldus concolor*, new species.

**Diagnosis.** Imaginary vertical plane at base of labium and at right angles to axis of body passing through eyes; basal segment of rostrum projecting onto concave prosternum, second segment approaching or reaching mesocoxae, apex of fourth extending onto base of abdomen. Bucculae well developed, uniformly produced, reaching base of head. Antennae 5-segmented; basal segment of each projecting slightly past apex of head, third segment 2.5–3.0 times length of second. Eyes contiguous with pronotum. Anteocular process present on each side (Fig. 50). Length of head before ocelli 0.6 of interocular width.

Anterolateral margins of pronotum weakly sinuous; small tooth at each anterolateral corner directed laterad; humeri scarcely produced, weakly emarginated. Width of scutellum at distal end of frena slightly more than one-half basal width; apex of scutellum reaching between imaginary line connecting anterolateral angles of fifth abdominal segment and similar line connecting posterolateral angles of same segment. Costal angles of coria projecting well past scutellar apex.

Mesosternum and metasternum carinate. Ostiolar sulci lacking; rugae short, each reaching 0.15 of distance from ostiole to lateral margin of metapleuron; evaporative areas small, confined to metapleura. Superior surface of last tarsal segments of hind legs flattened or concavely depressed in both sexes. Abdomen without mesial tubercle or spine at base. All trichobothria laterad of spiracular line. Basal plates rather evenly convex, without swollen areas. Width of pygophore 0.3 of maximum abdominal width.



Figs. 50-59. *Uvaldus concolor*, new species. 50. Habitus. 51. Genital plates, caudoventral view. 52. Same, caudal view. 53. Same, lateral view. 54. Spermatheca. 55. Pygophore, caudal view. 56. Genital cup. 57. Pygophore, ventral view. 58. Right paramere, lateral view. 59. Aedeagus, lateral view. Symbols: basal plate (bp); paramere (pa); proctiger (pr); paratergite 9 (pt9).

#### *Uvaldus concolor*, new species

Figs. 50-59

**Description.** Light brown above with fuscous to black punctation, usually with rufous to castaneous flecks on pronotum and scutellum and halos of the same color around punctures; cicatrices dark brown; moderate size callus in each basal angle of scutellum and elongated macule on disk of each corium usually ivory. Venter mostly dark brown; coxae, trochanters and rostrum brownish yellow; femora, tibiae and tarsi mottled in browns of varied intensity. Antennae uniformly light or dark brown.

Juga contiguous before tylus, leaving small indentation in apex of head, moderately reflexed marginally, especially at antecocular concavities (Fig. 50); anterocular process

on each side of juga short, obtuse. Punctuation rather dense, irregular. Width of head across eyes 2.4–2.5, length 1.75–1.95; length before ocelli 1.5–1.55; interocular width 1.35–1.5; distance across ocelli 1.1–1.2, between ocelli 0.8–0.9, from each ocellus to nearest eye 0.30–0.35. Segments I–V of antennae 0.65–0.7; 0.4–0.6; 1.3–1.35; 1.2–1.3; 1.6–1.7 long. Fourth antennal segment of males slightly clavate, its greatest diameter exceeding that of all other segments save first. Segments I–IV of labium 1.0; 1.6–1.7; 1.0–1.2; 1.0 long.

Anterolateral pronotal margins slightly sinuous, clearly reflexed. Punctuation less dense than on head, coarser, tending to cluster into short, transverse, streptococcal lines. Pronotal width at humeri 5.7–6.2, medial length 2.5–2.8.

Fovea in each basal angle of scutellum shallow, triangular, densely punctate, black; calloused macule contiguous with and about size of fovea, usually ivory. Punctuation similar to that on pronotum but denser. Scutellar width at base 3.6–3.9, length 4.0–4.3. Distal margin of each corium nearly straight, inner angle rounded; punctuation on endocorium and clavus as on pronotum, denser and finer on exocorium; membranes heavily fumose, each with 6 or 7 simple veins. Connexiva exposed, finely punctate, nearly uniform in color.

Posterior margins of basal plates sinuous from caudal view (Fig. 52), thickened, appearing somewhat separated from other plates (Fig. 53). Paratergite 9 channelized basally. Proximal part of spermathecal duct enlarged; spermathecal bulb small with 3 long diverticula (Fig. 54).

Sides of pygophore produced caudad, deeply sulcate; furrow dividing sides of pygophore from convex area ventrad of genital cup (Fig. 55); ventral border of genital cup convexly produced mesially, projecting horizontally. Distal half of proctiger scleritized, granular (Fig. 56). Parameres bilobed; dorsal lobe globose, smooth; ventral lobe thickly hirsute (Fig. 58).

**Types.** Holotype, ♂ labeled "Brazil: Est. Rio de Janeiro, Araruama XI. 1981. Coll. M. Alvarenga." Pygophore dissected. Deposited in the Carnegie Museum of Natural History, Pittsburgh.

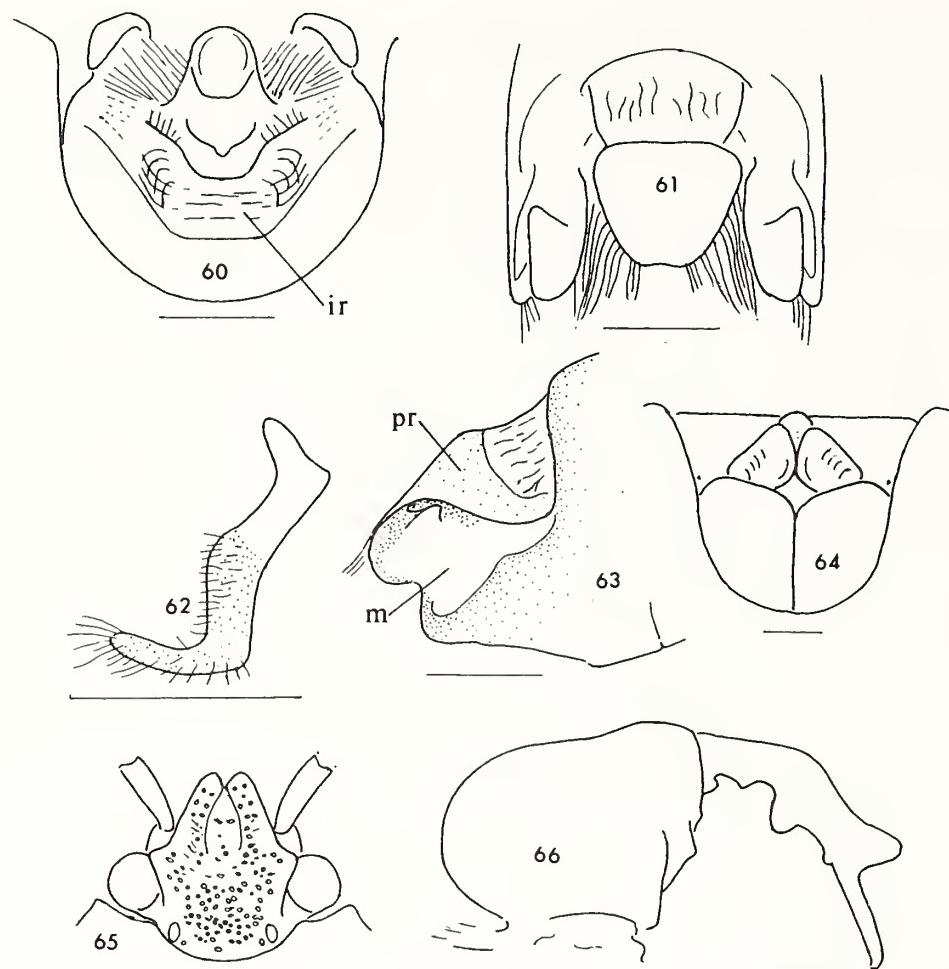
Paratypes 6♀♂ and 1♂ labeled same as holotype. (4♀♀ CMNH; 1♀ DAR; 1♀ DBT; 1♂ LHR.)

*Parochlerus* Breddin, 1904  
Figs. 60–66

*Parochlerus* Breddin, 1904:153. (Type species *Parochlerus latus* Breddin, 1904, by monotypy.)

**Diagnosis.** Lateral jugal margins tapering sharply from anteocular concavities to apex of head; juga convergent, projecting beyond tylus (Fig. 65); anteocular process before each eye rudimentary, obtuse. Length of head before ocelli two-thirds of width across eyes. Labium arising behind imaginary plane bisecting head at anterior limit of eyes; second rostral segment reaching slightly past mesocoxae; apex of rostrum on sternite 5. Antennae 5-segmented; basal segment protruding past apex of head; segment II nearly as long as segment III. Scutellar width at distal end of frena about one-half of basal width. Coria surpassing apex of scutellum. Metasternum carinate.

**Comments.** The generic name was an unfortunate choice because a close relation-



Figs. 60–66. *Parochlerus latus*. 60. Pygophore, caudal view. 61. Genital cup, dorsal view. 62. Paramere. 63. Pygophore, lateral view. 64. Genital plates, caudoventral view. 65. Head. 66. Aedeagus. Symbols: inferior ridge (ir); membranous area of pygophore (m); proctiger (pr).

ship to *Ochlerus* is implied. Only *Tetrochlerus* is obviously near *Parochlerus*, and these two genera appear to stand apart within the tribe.

*Parochlerus* is monotypic. Breddin's meager description of the type species, based on one female, is amplified by the following redescription, and the male is described. The species is known only from Peru and Amazonas, Brazil.

#### *Parochlerus latus* Breddin, 1904

Figs. 60–65

*Parochlerus latus* Breddin, 1904:153.

**Holotype.** Black to fuscous except as follows: edge of abdomen ventally, irregular narrow border on lateral margins of juga, scattered calluses and macules on dorsum and venter, basal 0.4 of last antennal segment, all yellowish; remainder of antennae, coxae, tarsi brown to castaneous; evaporative areas slate colored.

Head 2.7 wide at eyes, 2.2 long; width across ocelli 1.25. Punctuation rugose, diagonally so on juga. Segments I–V of antennae 0.9, 1.1, 1.6, 1.8, 2.1 long.

Pronotum 7.0 wide at humeri, 3.2 long mesially; anterolateral margins nearly

straight; humeri not produced laterally, obtusely angular; disk rugosely punctate behind cicatrices.

Scutellum 4.5 wide at base, 5.1 long; frena extending 0.6 distance from base to apex; disk somewhat rugose, especially basal part; apex moderately rounded, undifferentiated by color or punctuation. Coria punctured similarly to distal part of scutellum; membranes brown, each with about 10 simple or furcate veins. Connexiva moderately exposed, rather densely and strongly punctate.

Prosternum concave, mesosternum narrowly carinate mesially, both conspicuously punctured; metasternum carinate mesially (mostly destroyed by pin). Spiracles oval. Genital plates as in Figure 64.

The female holotype is labeled (a) "Peru, Amar," (b) "Parochlerus latus Breddin," (c) "Coll. Breddin," (d) "Typus," (e) "Holotypus." It is conserved in the Institut für Pflanzenschutzforschung, Eberswalde. The locality may not be interpreted correctly from the handwritten label. The original description indicates the holotype to be a male. Presumably the wrong sex symbol was used by Breddin or by the typesetter.

*Males.* Similar to female excepting genitalia.

Pygophore with apex V-shaped, mesial emargination of posterior margin truncate from caudal view (Fig. 60). Inferior ridge with U-shaped, mesial emargination; area between posterior pygophoral margin and inferior ridge not excavated. Pygophoral appendage at each posterolateral corner separated by membrane; mesial face of appendage concave; lateral face mostly membranous, only anterior and dorsal margins sclerotized from lateral view (Fig. 63). Posterolateral pygophoral corners, ventrad of appendages, acutely produced. Proctiger lacking tubercles; margin thickly fringed with long hair, particularly subapically (Fig. 61). Parameres delicate, each bent at right angle, somewhat flattened distally, bearing row of short hair proximad of bend and peripheral fringe of long hair distad of bend (Fig. 62). Theca and structures surrounding ejaculatory duct distad of theca sclerotized; membranous conjunctiva minuscule (Fig. 66).

#### *Tetrochlerus* Breddin, 1904

*Tetrochlerus* Breddin, 1904:153. (Type species *Tetrochlerus fissiceps* Breddin, 1904, by monotypy.)

*Diagnosis.* Differing from *Parochlerus* only in having 4-segmented antennae; segment III 0.6 length of segment II.

*Comments.* The type of *T. fissiceps* was not located. However, there is a specimen in the National Museum of Natural History, Washington, DC, that fits Breddin's short description exactly, including a length of 11.5 from the apex of the head to the tip of the hemelytral membranes, excepting that it is female. This specimen is described below and designated voucher specimen. It bears the labels (a) "Balzapamba (Ecuad). R. Haensch S.," (b) "Coll. Breddin," (c) "J. C. Lutz Collection, 1961," (d) "Tetrochlerus fissiceps Breddin."

The difference between *Tetrochlerus fissiceps* and *Parochlerus latus* in the number of antennal segments is hardly sufficient grounds to place each species in a separate genus. However, it seems best to leave this arrangement undisturbed until the male of *T. fissiceps* is known, since the male genitalia of the two species may differ sufficiently to justify retention of the present classification.

*Tetrochlerus fissiceps* Breddin, 1904

*Tetrochlerus fissiceps* Breddin, 1904:153.

*Voucher.* Dark brown except as follows: lateral margins of prothorax above and below, of coria basally, of connexiva and abdominal venter, rufous; submarginal macule in middle of connexival segments, flecks on abdominal venter and basal 0.4 of last antennal segment light brown to brownish yellow; anterior disk of pronotum, head, antennae (except base of last segment), femora and tibiae, fuscous to black.

Head 2.2 wide across eyes, 1.8 long; length before ocelli 0.7 width across eyes; dorsal punctuation dense, strong, diagonally rugose on juga; interocular width 1.3, each eye 0.45 wide, anterior-posterior diameter 0.55. Segments I-IV of antennae 0.7, 2.0, 1.3, 1.6 long. Segments II-IV of rostrum, 1.9, 1.3, 1.2 long; bucculae lacking anterior tooth.

Pronotum 6.0 wide at humeri, 2.7 long mesially; anterolateral margins slightly concave, narrowly reflexed; humeri not produced laterad; small tooth at anterolateral angles slightly acute; disk rugosely punctate behind cicatrices.

Scutellum 3.8 wide at base, 4.2 long; frena extending 0.6 of distance from base of scutellum to apex; basal disk rugosely punctate; apex slightly reflexed on each side, black-edged where reflexed. Connexiva narrowly exposed, less densely punctate than border of coria; punctures in macules black.

Prosternum concave; mesosternum and metasternum both carinate mesially and conspicuously punctate. Spiracles oval. Outline of genital plates as in *Parochlerus latus* (Fig. 64); basal plates convex, submarginally impressed at posterolateral angles.

Length 11.5

**Catulona, new genus**

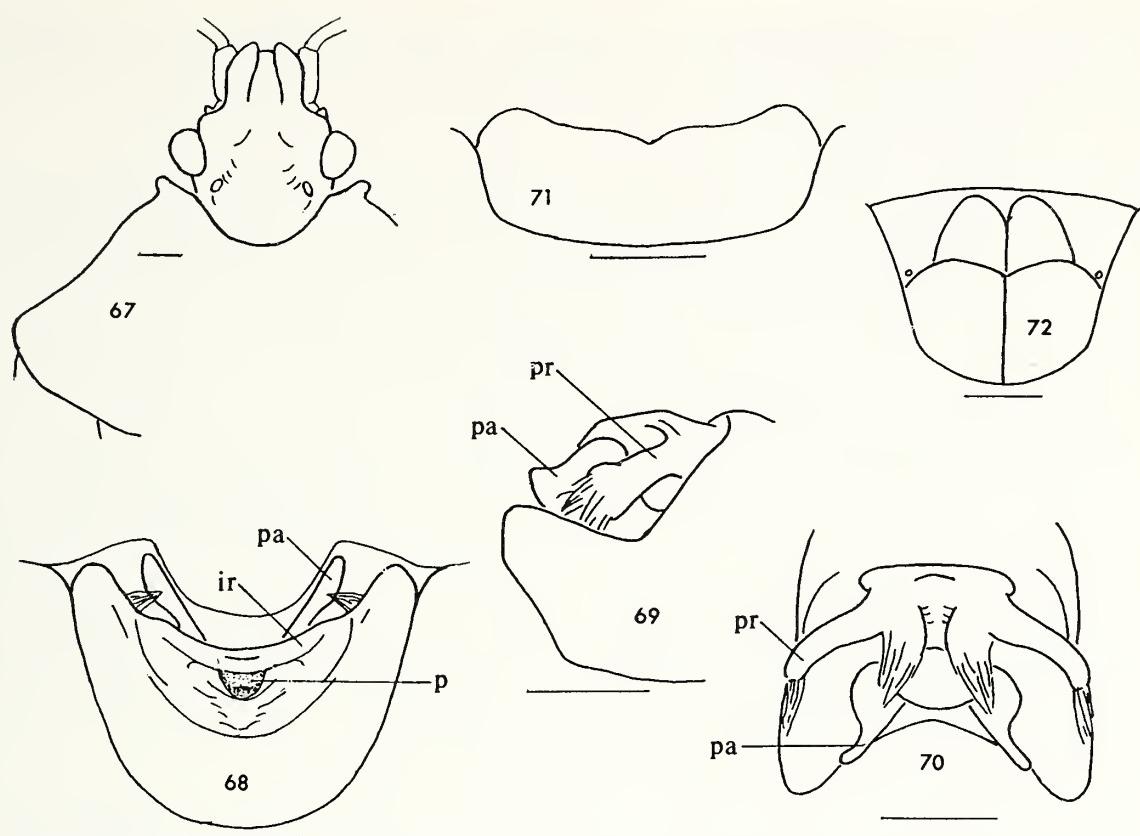
Figs. 67-78

Type species *Catulona pensa*, new species.

*Diagnosis.* Small tooth at anterolateral angles of pronotum reflexed, directed cephalad or anterolaterad. Juga as long as or slightly longer than tylus, their lateral margins briefly parallel between anteocular concavities and apex of head; each jugum with obtuse, rudimentary, anteocular process (Figs. 67, 73). Length of head before ocelli 0.7 of width across eyes. Eyes relatively small, width of each 0.2 of head width across eyes. Antennae 5-segmented; basal segment reaching apex of head; segments II and III subequal in length. Labium arising slightly behind imaginary plane bisecting head at anterior limit of eyes; segment II reaching mesocoxae; rostral apex on sternites 4 or 5. Humeri weakly produced, scarcely emarginated. Width of scutellum at distal end of frena slightly less than one-half of basal width. Costal angles of coria surpassing scutellar apex, lying above penultimate abdominal segment. Metasternum thinly carinate mesially. Second gonocoxae hidden (Figs. 72, 78).

Last abdominal tergum of male projecting mesially as thin, broad, convex process partially covering genital cup. Proctiger with pair of long, basal processes (Figs. 70, 75). Mesial pit in pygophore at base of and ectad to inferior ridge (Figs. 68, 74).

*Comments.* The tergal process distinguishes this genus among ochlerines, but either the pygophore must be removed or the hemelytra membranes displaced to see this character.



Figs. 67–72. *Catulona pensa*. 67. Head and pronotum. 68. Pygophore, caudal view. 69. Distal part of pygophore, lateral view. 70. Genital cup. 71. Pygophore, ventral view. 72. Genital plates, caudoventral view. Symbols: inferior ridge (ir); pit (p); paramere (pa); proctiger (pr).

### *Catulona pensa*, new species

Figs. 67–72

**Description.** Fuscous, usually with brownish dots and vermiciform marks on dorsal rugosities, and brownish yellow as follows: 3 basal spots on scutellum (1 mesial, 1 at each basal angle), small macule on disk of each corium, usually middle of each visible connexival segment, basal one-fourth to all of last antennal segment, coxae in part, extension of connexival macules as broken lateral border along abdominal venter, crescent or spot bordering some or all of spiracles mesially. Length 10.7–11.0.

Vertex of head and base of tylus quite swollen (Fig. 67). Punctuation on dorsum of head fine to obscure. Juga and tylus of females subequal in length, each separately rounded; juga exceeding tylus in male, leaving nearly square notch in apex of head. Width of head across eyes 2.2–2.4, length 2.0–2.5. Interocular distance 1.2–1.4. Distance across ocelli 1.25–1.4, between ocelli 1.0–1.1. Segments I–V of antennae 0.6–0.7, 0.8–0.9, 0.8–1.0, 1.2–1.3, 1.8–2.1 in length. Last 3 segments of rostrum 2.0–2.3, 1.6–1.9, 1.5–2.0 in length.

Anterolateral pronotal margins slightly sinuous, slightly reflexed; triangular tooth at each anterolateral angle directed cephalad, projecting past posterior margin of eye (Fig. 67). Disk somewhat rugose. Width of pronotum at humeri 5.8–6.3, mesial length 2.5–2.8.

Basal width of scutellum 3.7–4.0, length 4.0–4.6. Membranes of hemelytra dark, with about 9 simple or furcate veins each, those toward costal margin usually faint. Connexiva narrowly exposed.

Evaporative area on each pleuron small, with ridges fanning out from orifice and extending little past auricle. Mesial, longitudinal sulcus on abdominal venter broad, shallow, extending from base over several or all sternites.

Genital plates as in Figure 72.

From caudal view, pygophoral emargination broad, semi-circular (Fig. 68). Dorsal margin of inferior ridge evenly concave; tuft of hair projecting mesad located at each lateral limit of inferior ridge and just entad of posterior pygophoral margin; area between posterior pygophoral margin and inferior ridge sloping to mesial pit at base of inferior ridge. From ventral view, pygophoral emargination shallow, slightly sinuous between mesial notch and posterolateral corners (Fig. 71). Proctiger bearing long, depressed, basal process on each side, these curving posteroventrad, fringed apically with long hairs (Fig. 69); apex of proctiger somewhat expanded and strongly impressed; a pair of protuberances clothed in long hairs located between basal processes and apical impression (Fig. 70). Parameres compressed, concave laterally, convex mesially, bilobed apically; posterior lobe acute, anterior lobe broadly rounded.

*Types.* Holotype, ♂ labeled "Brazil, Rio de Janeiro; Repressa Rio Grande, December 1977, M. Alvarenga." Deposited in the Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Paratypes, 4♀, 3♀ labeled "Brazil, Bahia: Encruzilhada. 960 m. Nov. 1972. M. Alvarenga" (2 AMNH, 1 LHR) and 1♀ labeled "Fry Coll. 1905.100" (BMNH).

*Comments.* The swollen vertex of the head will separate this species from the one other species of the genus. The swollen vertex also occurs in a few species of *Lincus*.

#### Catulona apaga, new species

Figs. 73–78

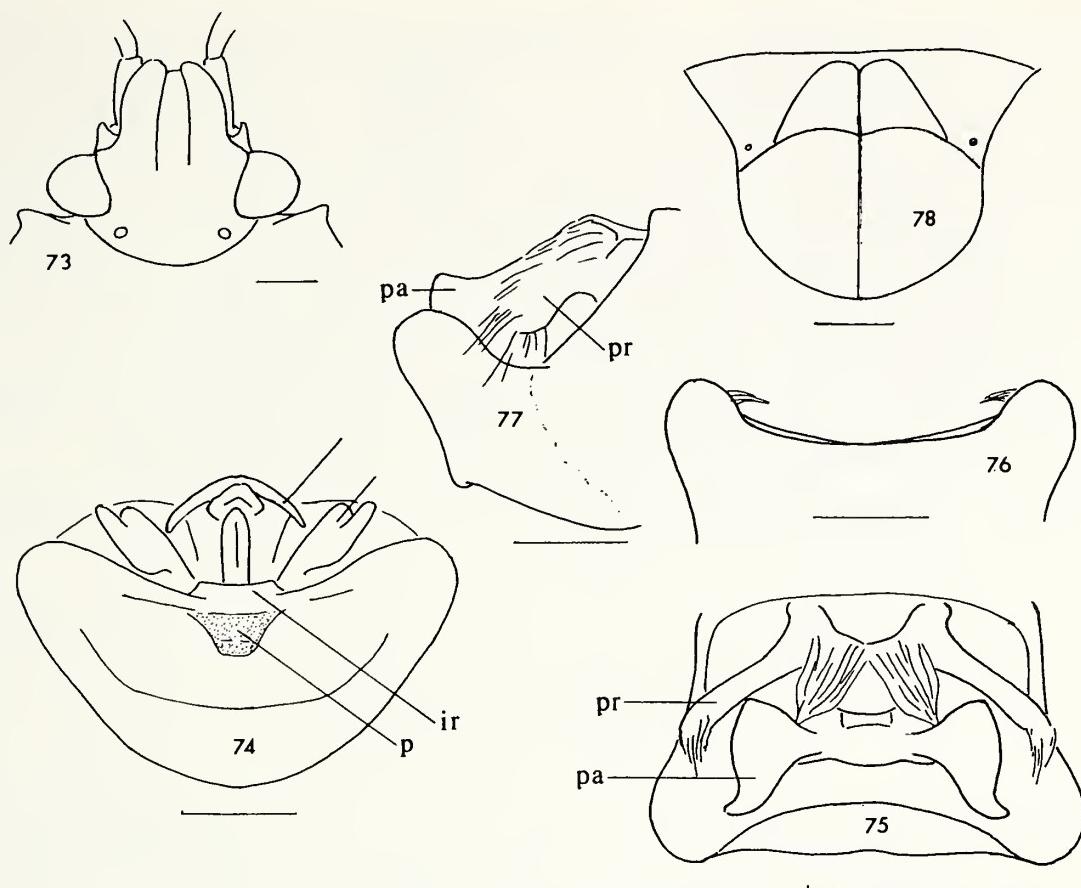
*Description.* Fuscous with brownish yellow as follows: at base of scutellum large mesial spot and sometimes small spot at each basal angle, small spot on disk of each corium and at mesial edge of each spiracle, short vermiform line on meson of pronotum and several such markings on abdominal venter, submarginal lateral line on each sternite, fifth antennal segment. Length 14.0–14.3.

Neither vertex of head nor base of tylus tumescent. Dorsum of head rugosely punctate, transversely to diagonally so on juga and tylus except apically. Juga surpassing tylus, somewhat convergent apically (Fig. 73). Width of head across eyes 3.0–3.1, length 2.5–2.6. Interocular distance 1.6. Distance across ocelli 1.45–1.5, between ocelli 1.1. Segments I–V of antennae 0.9, 1.2–1.3, 1.2–1.3, 1.5–1.6, 1.7 long. Last 3 rostral segments 2.5, 2.0, 1.9 long.

Anterolateral margins of pronotum shallowly concave, tooth at anterolateral angles subtriangular, directed anterolaterad. Disk rugose, strongly punctate. Width of pronotum at humeri 7.5–7.6, length at meson 3.4–3.5.

Scutellum 4.8 wide at base, 5.5–5.6 long. Membranes of hemelytra dark, nearly opaque, each with about 12 simple or furcate veins. Connexiva rather broadly exposed.

Evaporative areas and basal plates similar to type species (Fig. 78). From caudal view, posterior pygophoral margin forming obtuse, concave emargination; surface entad of posterior margin sloping regularly to inferior ridge; deep, mesial, subtriangular pit located at base of inferior ridge, a shallow sulcus extending from pit toward



Figs. 73–78. *Catulona apaga*. 73. Head and anterior pronotal margin. 74. Pygophore, caudal view. 75. Genital cup. 76. Posterior pygophoral margin, ventral view. 77. Distal part of pygophore, lateral view. 78. Genital plates, caudoventral view. Symbols: inferior ridge (ir); pit (p); paramere (pa); proctiger (pr).

posterior margin (Fig. 74). From ventral view, posterior pygophoral margin shallowly and evenly concave (Fig. 76), from dorsal view slightly sinuous (Fig. 75). Proctiger with pair of large, compressed, basal processes, each directed posterolaterad, fringed apically with long hairs; pair of large, contiguous protuberances just distad of origin of processes, each clothed in long hairs. Parameres compressed, lateral surface of each concave, mesial surface unevenly convex, paramere-head entire, posterodorsal edge forming acute tooth (Fig. 75).

**Types.** Holotype, ♂ labeled (a) "Brasilia" and (b) "Coll. F. Salvator." Deposited in the National Museum of Natural History, Washington, DC.

Paratypes, 3♀♀. 1♀ labeled "Strum, Brazil" (LHR); 1♀ labeled (a) "Brasilia" and (b) "Coll. F. Salvator" (SZCU); and 1♀ labeled "Beske Rio" (RNH).

**Comments.** This species differs from *Catulona pensa* in the moderately convex rather than inflated vertex, in larger size and in details of the genitalia.

**Cromata, new genus**  
Figs. 79, 80

Type species *Cromata ornata*, new species.

**Diagnosis.** Second rostral segment projecting past mesocoxae; apex of rostrum on

last sternite; labium arising near or on imaginary plane bisecting head at anterior limit of eyes. Anteocular margins of head lacking well developed processes; lateral jugal margins subparallel or parallel between anteocular concavity and apex of head; juga as long as or longer than tylus (Fig. 79). Width of reticulated part of each eye 0.2 width of head across eyes. Length of head anterior to ocelli 0.7–0.8 width of head across eyes. Antennae 5-segmented; basal segment not or scarcely exceeding apex of head; segment II more than one-half length of segment III. Anterolateral margins of pronotum strongly reflexed, especially toward apex; small tooth present at each anterolateral angle. Width of scutellum at distal end of frena a little less than one-half of basal width. Costal angles of coria surpassing apex of scutellum, lying above penultimate abdominal segment. Metasternum thinly carinate mesially.

*Comments.* This genus appears most nearly related to *Coranda*, new genus, but differs in the form of the head and pronotum.

**Cromata ornata, new species**

Figs. 79, 80

*Description.* Usually ochraceous with rufous borders along anterolateral margins of pronotum, costal margins of coria basally, lateral margins of abdomen ventrally; connexiva, femora distally and tibiae proximally also rufous, as is occasionally nearly all of dorsum. Punctuation, antennae, tibiae except at base, preapical femoral band, large marginal spot at abdominal incisures, band on each side of transverse connexival sutures and pair of spots on apex of scutellum all dark brown to black.

Head across eyes 2.2–2.5 wide, 2.0–2.5 long. Segments I–V of antennae 0.7–0.8, 0.7–1.0, 1.1–1.3, 1.3–1.6, 2.0–2.2 long. Segments II–IV of rostrum subequal in length, 2.3–2.7. Juga usually a little longer than tylus, their lateral margins sharply reflexed, subparallel between anteocular concavities and apex of head (Fig. 79).

Anterolateral margins of pronotum slightly sinuous from dorsal view; pronotal width at humeri 5.7–6.6, length mesially 2.6–3.2; disk divided along meson by impunctate line that continues for entire length of scutellum.

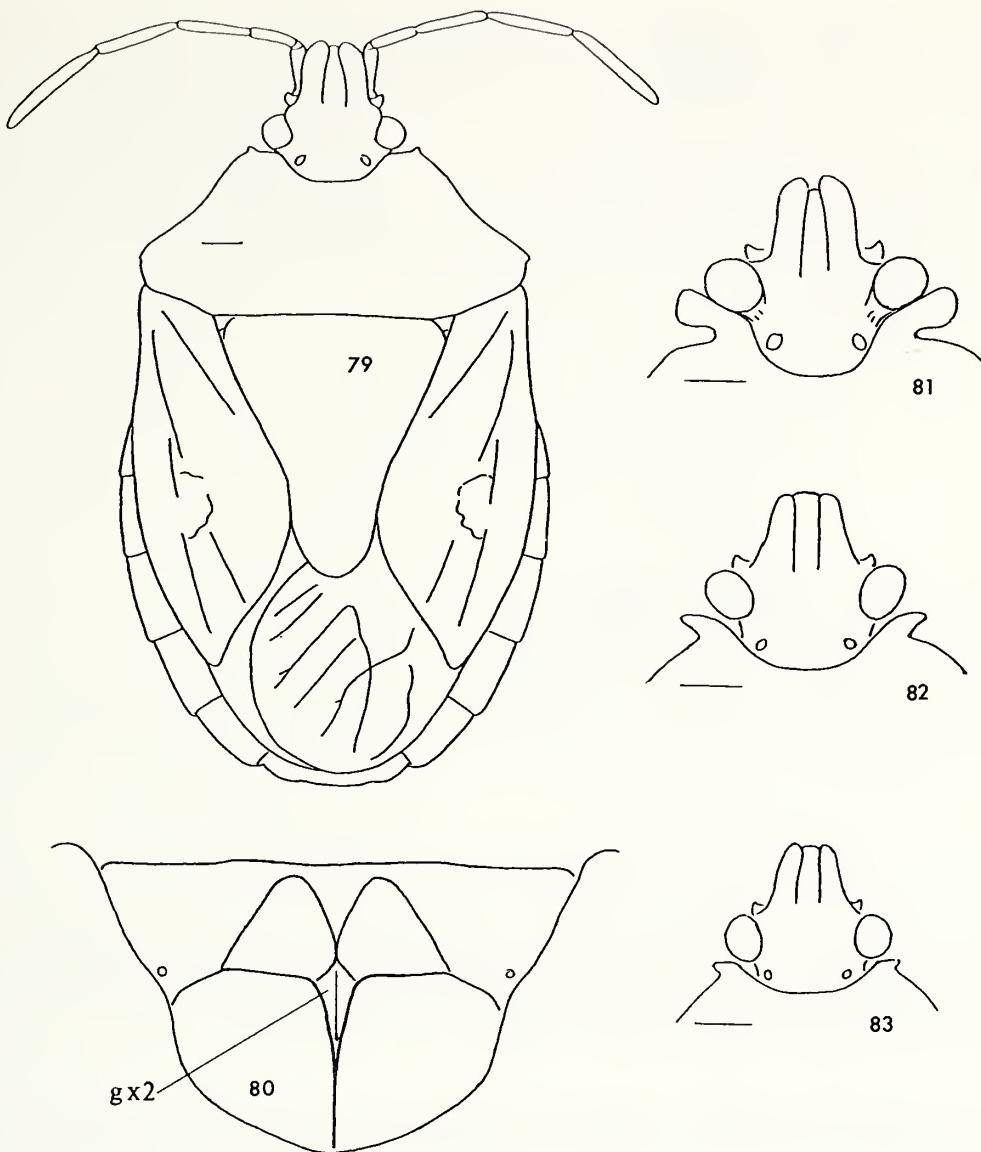
Scutellum 3.6–4.1 wide at base, 4.0–4.6 long; foveae in basal angles small, consisting of a few clustered punctures, isolated by an impunctate band; apex reflexed slightly at large, dark, marginal spots. Costal margins of coria reflexed basally; large, impunctate lacuna present on disk of each corium; membranes lightly fumose, each with about 7 veins. Connexiva broadly exposed.

Gonocoxae 2 tectiform where exposed (Fig. 80).

*Types.* Holotype, ♀ labeled "Brazil, Espírito Santo: Linhares, Sept. 1972, M. Alvarenga." Deposited in the American Museum of Natural History.

Paratypes, 8♀. 1♀ labeled same as holotype (AMNH); 1♀ labeled "Brazil, Mato Grosso, Lat. 12°31' and Long. 55°37', Sinop, October, 1974. M. Alvarenga" (AMNH); 4♀ labeled "Brazil, Bahia, Encruzilhada, 960 m. Nov. 1972, M. Alvarenga" (2 AMNH, 2 LHR); 1♀ labeled "BRAZIL: São Paulo, São Paulo, 3 February 1974, Coll. V. N. Alin" (DAR); 1♀ labeled "Encruzilhada, Bahia, Brazil, XIII 1980" and "A. Martinex e M. Alvarenga" (LHR).

*Comments.* Among ochlerines, this species is the most colorful. Even so it is rather drab.



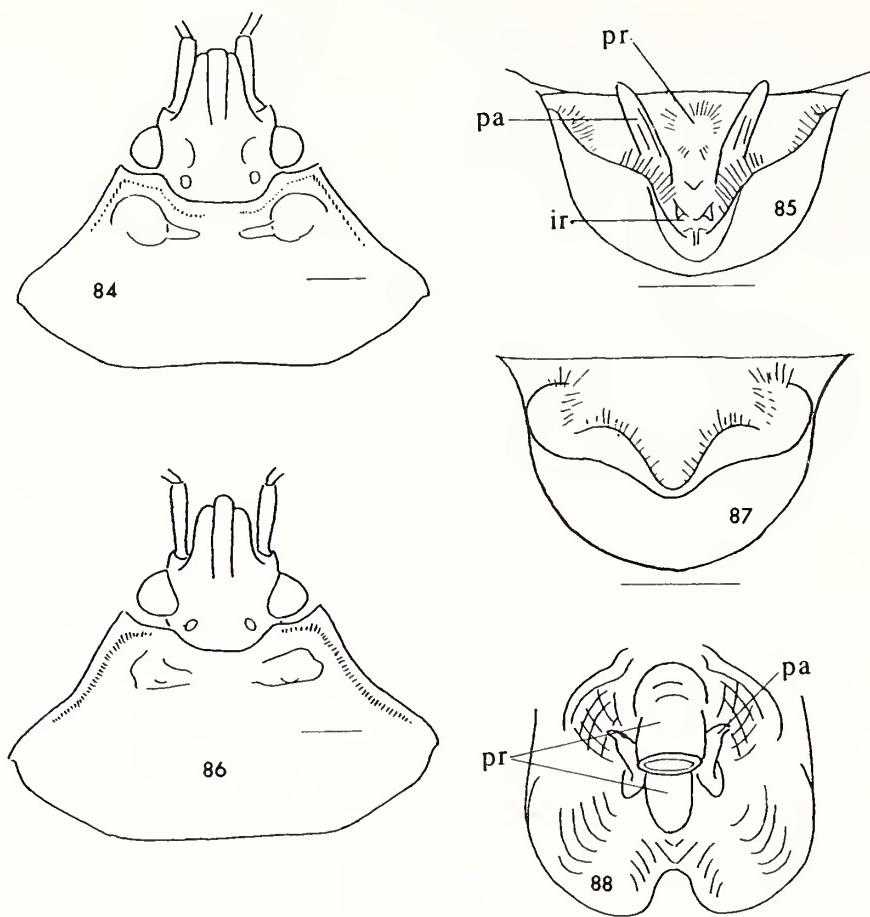
Figs. 79–83. 79, 80. *Cromata ornata*. 79. Habitus. 80. Genital plates, caudoventral view. 81–83. Head and anterior part of pronotum. 81. *Lincus securiger*. 82. *L. styliger*. 83. *L. dentiger*. Symbol: 2nd gonocoxae (gx2).

*Lincus* Stål, 1867  
Figs. 81–83

*Lincus* Stål, 1867:524; Stål, 1872:12, 14; Rolston, 1983a:2–7 (revision). (Type species *Pentatoma rufospilata* Westwood, 1837, by original designation.)

*Minilincus* Ruckes, 1958:14–15 (synonymized by Rolston, 1983a). (Type species *Minilincus parvulus* Ruckes, 1958, by original designation.)

*Diagnosis.* Labium originating behind imaginary plane bisecting head at anterior limit of eyes; second rostral segment extending a little past mesocoxae; rostral apex on or beyond penultimate sternite. Antennae 5-segmented, basal segment reaching or surpassing apex of head. Juga as long as or longer than tylus, sometimes contiguous apically. Length of head before ocelli 0.6–0.8 of width across eyes. Scutellum 0.4–0.5 as wide at distal end of frena as at base. Coria extending past apex of scutellum.



Figs. 84–88. 84, 85. *Coranda picipes*. 84. Head and pronotum. 85. Pygophore, caudal view. 86–88. *Coranda castana*. 86. Head and pronotum. 87. Pygophore, caudal view. 88. Genital cup. Symbols: inferior ridge (ir); paramere (pa); proctiger (pr).

Metasternum flat, or weakly tectiform, sometimes with weak, medial carina for only part of its length.

*Comments.* Most species of *Lincus* are recognizable as members of the genus by their well-developed pronotal lobes (Figs. 81, 82), although several species have unremarkable pronotal lobes (Fig. 83). This is one of the largest ochlerine genera with 35 described species (Rolston, 1983a, 1989; Dolling, 1984). Some of these species are known to be of economic importance as vectors of plant diseases. The genus is widely distributed in Central and South America.

#### **Coranda, new genus**

Figs. 84–88

Type species *Melanodermus picipes* Stål, 1872.

*Diagnosis.* Anterolateral angles of pronotum acute, projecting forward beyond base of eyes; anterolateral margins prominently reflexed, especially toward apex (Figs. 84, 86). Second rostral segment reaching anterior limit of metacoxae; rostral apex lying on last abdominal sternite; labium arising on or near imaginary plane bisecting head at anterior limit of eyes. Anteocular process absent; lateral jugal margins tapering from anteocular concavity to apex of head; tylus longer than juga. Width of reticulated part of each eye 0.25 as wide as head across eyes; length of head before ocelli 0.7–0.8 of head width across eyes. Antennae 5-segmented; basal segment surpassing apex

of head; segment II one-half length of segment III; width of scutellum at distal end of frena a little less than one-half of basal width. Costal angle of each corium surpassing apex of scutellum, lying above penultimate abdominal segment. Metasternum thinly carinate mesially.

*Comments.* Members of this genus resemble *Stalius tartareus* in the form of the pronotum and size. However, *Stalius* is among those genera with a relatively broad and long scutellum. *Coranda* seems closely related to *Cromata* but differs in the form of the head and pronotum.

*Coranda picipes* (Stål, 1872), New Combination  
Figs. 84, 85

*Melanodermus picipes* Stål, 1872:14.

*Description.* Dark castaneous to fuscous dorsally with many interstitial rugae, basal one-third of last antennal segment and marginal macule on each connexival segment light castaneous to light brownish yellow. Venter castaneous to fuscous, generously mottled with yellowish brown. Tibiae of dark yellowish brown legs annulated with 3 fuscous bands: 1 at base, 1 at apex, and 1 intermediate, these bands increasing progressively in width from base to apex.

Head 1.9–2.2 wide across eyes, 1.7–1.9 long. Interocular width 1.1–1.25; distance across ocelli 0.85–0.95. Anterior-posterior diameter of eyes slightly greater than width, diameter 0.5, width 0.45. Segments I–V of antennae 0.8, 0.6, 1.1–1.2, 1.1, 1.6–1.8 long. Segments II–IV of rostrum about 2.5–2.6, 2.0–2.2, 2.0–2.2 in length.

Pronotum 4.8 wide at humeri, 1.9–2.2 long mesially. Cicatrices subcircularly elevated laterally.

Scutellum 2.9–3.1 wide at base, 3.2–3.5 long; apex slightly reflexed on each side. Distal margin of each corium slightly convex; membranes heavily fumose, each with 9 simple veins. Connexiva broadly exposed.

Mesial emargination of pygophore deep from caudal view, sinuously V-shaped. Parameres visible from caudal view, divergent, straight, their posterior surface sulcate (Fig. 85). Inferior ridge divided mesially, with small, triangular tooth on each side of division.

Length 9.8.

*Distribution.* Colombia (Bogotá), Peru (La Libertad).

*Comments.* The holotype of *Melanodermus picipes*, which now lacks a pygophore, was examined. It is conserved in the Naturhistoriska Riksmuseet, Stockholm.

This species is transferred from *Ochlerus* (=*Melanodermus*) because the short and subapically narrow scutellum (relative to *Ochlerus*), the long rostrum, and other characteristics are contraindicative of *Ochlerus*. From the other species of the genus, *C. picipes* is particularly distinguished by the form of the pygophore and fuscous coloration.

*Coranda castana*, new species  
Figs. 86–88

*Description.* Brown to light castaneous dorsally; cicatrices and densely punctate band on each side of vertex fuscous; border anterior to and laterad of cicatrices and

much of head dark castaneous; connexiva alternated, with yellowish median macule traversing all or part of each segment. Abdominal venter dully mottled in shades of brown. Legs and rostrum brownish yellow; basal segment of antennae light brown, segments II-IV light brown (V missing).

Head 2.0 wide across eyes, 1.9 long; length of head before eyes 0.75 of width across eyes. Interocular width 1.05, distance across ocelli 0.85. Each eye about 0.5 wide; anterior-posterior diameter equal to width. Segments I-IV (V missing) of antennae 0.8, 0.5, 1.1, 1.2 long. Segments II-IV of rostrum 3.2, 2.1, 2.1 long.

Pronotum 5.1 wide at humeri, 2.2 long mesially.

Scutellum 3.0 wide at base, 3.3 long; apex slightly reflexed on each side. Distal margin of each corium slightly convex; membranes heavily fumose, each with 9 simple veins. Connexiva broadly exposed.

Dorsal margin of pygophore tumescent on each side of mesial emargination (Figs. 87, 88). Parameres with stout apical hook on anterior edge. Inferior ridge flattened, V-shaped from dorsal view.

Length 9.7.

*Type*. Holotype, ♂ labeled (a) "Santa Jnez [sic] (Ecuad.) R. Haensch S.," (b) "coll. Breddin." Deposited in the Akademie der Landwirtschaftswissenschaften, Eberswalde. No paratypes.

*Comment*. The trisinuate posterior pygophoral margin and castaneous coloration distinguish this species from *C. picipes*, which has a single medial emargination in the posterior pygophoral margin and fuscous coloration.

### *Brachelytron* Ruckes, 1958

*Brachelytron* Ruckes, 1958:17-19. (Type species *Brachelytron angelicus* Ruckes, 1958, by original designation.)

*Diagnosis*. Brachypterous, coria truncate distally above tergum 4, not reaching broadly rounded scutellar apex above tergum 5. Ocelli present but small. Antero-lateral angles of pronotum curving around head, projecting anteriorly beyond eyes. Anteocular processes short, acute. Juga surpassing tylus. Antennae 5-segmented, first segment extending only to apex of head. Labium arising behind imaginary plane bisecting head at anterior limit of eyes; second rostral segment reaching mesocoxae. Metasternum carinate.

*Comments*. The genus is monotypic, represented so far by a single specimen from Brazil.

Brachypterous forms occur in two other genera, *Alathetus* and *Miopygium*. Of these, only the latter genus is sympatric. In addition to the distinguishing characteristics given in the key, *Miopygium* differs from *Brachelytron* in having 4-segmented antennae, the basal segment of which projects beyond the apex of the head, and a shorter rostrum, with the second segment reaching just beyond the procoxae.

### CODENS FOR PARATYPE DEPOSITION

AMNH, American Museum of Natural History, New York

BMNH, British Museum (Natural History), London

CAS, California Academy of Sciences, San Francisco

- CMNH, Carnegie Museum of Natural History, Pittsburgh  
DAR, D. A. Rider collection  
DBT, D. B. Thomas, Jr. collection  
HDE, H. D. Engleman collection  
LHR, L. H. Rolston collection  
NMNH, U.S. National Museum of Natural History, Washington  
RMB, R. M. Baranowski collection  
RNH, Riksmuseum van Natuurlijke Historie, Leiden  
SZCU, Systematic Zoology, Charles University, Prague.

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Type material was made available by Richard C. Froeschner, P. M. Giachino (Museo Regionale de Scienze Naturali, Torino), A. Kaltenbach (Naturhistorisches Museum Wien), Per Lindskog (Naturhistoriska Riksmuseet), G. Petersen (Akademie der Landwirtschaftswissenschaften der D.D.R.) and Randall T. Schuh.

Prof. Carlo Vidano (Universita Delgi Studi) attempted to examine the relevant material in the Spinola collection before the collection was moved to the Museo Regionale di Scienze Naturali, Torino. His efforts are appreciated.

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To all of these colleagues I am grateful. To the curators who unsuccessfully searched their collections for Breddin type material, I am also grateful.

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REVISION OF THE GENUS *THYANTA* STÅL, 1862  
(HETEROPTERA: PENTATOMIDAE)  
II. NORTH AMERICA, CENTRAL AMERICA,  
AND THE WEST INDIES

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*Abstract.*—The species of the pentatomid genus *Thyanta* Stål occurring north of South America are revised. All northern hemisphere species belong to the subgenera *Thyanta* and *Argosoma* Rider. Diagnoses are given for the genus, subgenera, and the 14 included species and subspecies. The subspecies *accerra* McAtee is transferred from *T. pallidovirens* (Stål) to *T. custator* (Fabricius). The following new synonymy is recognized (junior synonym in parentheses): *T. custator accerra* McAtee, 1919 (= *T. pallidovirens spinosa* Ruckes, 1957a), *T. pallidovirens* (Stål, 1859) (= *T. pallidovirens setosa* Ruckes, 1957a), and *T. maculata* (Fabricius, 1775) (= *T. casta* Stål, 1862b). Lectotype designations are made for *Cimex maculatus* Fabricius, *Pentatoma obsoleta* Dallas, *P. pallidovirens*, *T. casta*, and *T. pseudocasta* Blatchley. *Thyanta planifrons* Ruckes is reported from the United States for the first time. A key is provided for the subgenera, species, and subspecies that occur north of South America.

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The genus *Thyanta* is restricted to the western hemisphere and is one of several fairly large genera in the nominate tribe and subfamily of the Pentatomidae. Historically, identifications in this genus have been difficult. In fact, Jensen-Haarup (1928) commented "The species are very variable, but at the same time inter se much similar both as to colour and sculpture, and also regarding the genital segments; a strict separation of most of the species is, therefore, rather difficult, if not rich and fresh materials of species and specimens are at hand." There has been no recent treatment of the entire genus, the last being that of Jensen-Haarup in 1928. Malloch (1919), Blatchley (1926), and Torre-Bueno (1939) all reviewed portions of the genus, but their works have become outdated largely due to the addition of many new species and subspecies (Ruckes, 1952, 1956, 1957a, b, c; Rider and Chapin, 1991).

The genus *Thyanta* is one of a group of pentatomine genera characterized by the lack of a spine or tubercle on the third (second visible) abdominal sternite. Rolston and McDonald (1984) provided a key to separate those genera occurring in the Western Hemisphere north of South America. Because there are many species and many of them are difficult to distinguish, the genus has been divided into two groups according to geographical regions. The present paper reviews those species known to occur north of South America. The South American species of *Thyanta* were recently revised by Rider and Chapin (1991).

Care should be maintained when using the key to species. It is important to have fresh, mature specimens. After death, specimens tend to become greasy and discolored, making their determinations rather tentative. In the key, when certain characters

are described as black or piceous, the true structural color is black, not just darkened due to discoloration. Teneral specimens and specimens of brown forms often have darkened areas that may be misleading when working through the key. Most characters of the genitalia can be seen without dissecting the specimen; however, accurate determinations may require some dissection. In many cases there are no reliable characters to separate females. The only way to identify females in these instances is by association with males or sometimes by geographical distribution.

When label data is cited in the text, each letter in parentheses represents a different label with (a) being closest to the specimen. Museum acronyms used in the text are defined in the acknowledgements. All measurements are in millimeters. Measurements in parentheses are of the holotype.

### *Thyanta* Stål 1862

*Thyanta* Stål, 1862a:58; Stål, 1867:529; Stål, 1872:34–35; Distant, 1880:65; Summers, 1898:45; Kirkaldy, 1909:94; Van Duzee, 1917:51; Blatchley, 1926:104, 112–113; Jensen-Haarup, 1928:185–186; Furth, 1974:21–22; Froeschner, 1981:71; McPherson, 1982:48, 76–77; Rolston and McDonald, 1984:74, 76; Froeschner, 1988: 592.

*Type species.* *Cimex perditor* F., 1794 (by subsequent designation, Kirkaldy, 1909: XXX).

*Diagnosis.* Third (second visible) abdominal sternite lacking medial spine or tubercle. Each ostiolar ruga sulcate proximally, reaching at least three-fourths distance from mesial margin of ostiole to lateral margin of metapleuron. Bucculae evanescent or arcuately truncate at posterior terminations. Juga and tylus usually subequal in length; rostrum reaching at least to metacoxae. Femora unarmed; superior surface of each tibia usually sulcate. Width of scutellum at distal end of frena two-fifths or less basal scutellar width. Each paramere narrowly rounded to acute apically, lacking denticles, usually lacking lateral lobe, rarely with spinose lateral lobe.

*Comments.* The genus *Thyanta* is closely related to two other pentatomine genera, *Cyptocephala* Berg and *Tepa* Rolston and McDonald, from which it can be separated reliably only by differences in the male genitalia. In all northern hemisphere species of *Thyanta*, the head of each paramere lacks a lateral lobe. In *Cyptocephala* and *Tepa*, the parameres have well-developed lateral lobes. *Cyptocephala* further differs from *Tepa* and *Thyanta* by having minute denticles between the lateral lobe and the apex of the paramere. The parameres of species of *Tepa* and *Thyanta* lack denticles.

Jensen-Haarup (1928) described the subgenus *Parathyanta* within *Thyanta*. Rolston and McDonald (1984) placed *Parathyanta* in the synonymy of *Cyptocephala*. At the same time, they transferred 4 species from *Thyanta* to *Cyptocephala* and 6 species from *Thyanta* to *Tepa*. The species of both *Cyptocephala* and *Tepa* have been reviewed recently (Rolston, 1972, 1986; Rider, 1986a).

The genus *Thyanta* is divided into three subgenera: *Argosoma* Rider, *Phacidium* Breddin, and *Thyanta*. All 8 species of the subgenus *Phacidium* are restricted to South America and have been treated in an earlier paper (Rider and Chapin, 1991). *Argosoma* contains 20 species, 6 of which are known to occur outside South America. The nominate subgenus contains 9 species of which 7 are known to occur in the area covered by the present paper.

KEY TO SUBGENERA OF *THYANTA* STÅL

1. Dorsal surface relatively shiny, glossy; punctures relatively large, sparse; pygophoral opening relatively large; posteroventral surface of pygophore produced into small, blunt, chin-like protuberance; ectal surface of each paramere concave; spermathecal bulb globose ..... *Argosoma* Rider
- Dorsal surface appearing matte, not shiny; punctures relatively small, dense; pygophoral opening relatively small, posteroventral surface of pygophore not produced into blunt, chin-like protuberance; ectal surface of each paramere convex; spermathecal bulb globose or digitiform ..... 2
- 2(1). Pygophoral opening subtended by semicircular or rectangular impression; posterior margin of pygophore with medially emarginate production in middle; theca large, subtriangular, with small protuberance on each side near lateral dorsal margin; proximal end of sclerotized rod cone-shaped; spermathecal bulb digitiform ..... *Thyanta* Stål
- Posteroventral surface of pygophore smoothly arcuate or with distinct sulcus, not with semicircular or rectangular impression; posterior margin of pygophore nearly transverse, lacking medial production; theca reniform, lacking protuberances on lateral dorsal margin; proximal end of sclerotized rod may be slightly swollen, but not cone-shaped; spermathecal bulb globose ..... *Phacidium* Breddin

KEY TO SPECIES OF *THYANTA* OCCURRING NORTH OF SOUTH AMERICA

1. Anterolateral margins of pronotum piceous; mesial angle of each pronotal cicatrice black ..... 2
- Anterolateral margins of pronotum not piceous; coloration of mesial angle of each pronotal cicatrice variable, often immaculate ..... 3
- 2(1). Piceous markings along anterolateral pronotal margins relatively broad, usually easily visible from dorsal view; pygophoral opening subtended by semicircular impression; general form relatively broad (eastern U.S.) ..... *calceata* (Say)
- Piceous markings along anterolateral pronotal margins relatively narrow, not easily visible from dorsal view; pygophoral opening subtended by rectangular impression; general form relatively narrow (coastal plain from central Louisiana to Florida to New York) ..... *custator custator* (Fabricius)
- 3(1). Humeral angles rounded to angulate, but never spinose ..... 4
- Humeral angles distinctly spinose ..... 6
- 4(3). Dorsal punctuation minute, dense, surface appearing matte; pygophoral opening subtended by rectangular impression; ectal surface of each paramere convex, lacking dorsomedial concave surface (Fig. 34); spermathecal bulb digitiform (Fig. 47) ..... 5
- Dorsal punctuation coarse, sparse, surface glossy; posteroventral surface of pygophore produced into blunt chin-like protuberance; each paramere with dorsomedial surface concave (Fig. 126); spermathecal bulb globose (Fig. 136) ..... 10
- 5(4). Postspiracular black spot usually present on each side of each abdominal sternite and usually larger in diameter than adjacent spiracle; if absent or smaller than spiracle, then humeral angles usually angulate (eastern U.S.) ..... *custator accerra* McAtee (part)
- Postspiracular area of each abdominal sternite immaculate; or, if black spot present, then spot is usually smaller in diameter than adjacent spiracle; humeral angles rounded, never angulate (western U.S.) ..... *pallidovirens* (Stål)
- 6(3). Mesial angle of each pronotal cicatrice often marked with black; posterolateral angle of each abdominal sternite usually black; pygophoral opening subtended by

- semicircular impression, posterior margin with distinct medial slit (Fig. 71) .... 7
- Without above black markings; pygophoral opening subtended by rectangular impression, posterior margin straight, concave, or sinuous, without medial slit (Fig. 41) (southwestern U.S.; Mexico; Guatemala) .... *custator accerra* McAtee (part)
- 7(6). Complete or partial transhumeral reddish band usually present; both anterolateral and posterolateral angles of each abdominal sternite usually piceous ..... 8
- Reddish band between humeral angles usually absent; each abdominal sternite with anterolateral angle immaculate, each posterolateral angle with at most a small black spot ..... 9
- 8(7). Humeral angles directed anterolaterad, usually approaching a 45-degree angle with longitudinal axis of body (Fig. 63) (southern U.S. to northern Argentina) .... *perditor* (Fabricius)
- Humeral angles directed primarily laterad and only slightly anterad (Fig. 78) (Baja California, Mexico) ..... *spectabilis* Ruckes
- 9(7). Yellow anterolateral pronotal margins contrasting with rest of pronotum; pronotal cicatrices immaculate; usually smaller than 9.0 mm long by 6.0 mm wide (Cuba; British West Indies) ..... *cubensis* Barber & Bruner
- Anterolateral pronotal margins concolorous with rest of pronotum; mesial angle of each pronotal cicatrice usually black; usually larger than 9.0 mm long by 6.0 mm wide (Revillagigedo Islands, Mexico) ..... *serratulata* Ruckes
- 10(4). Southwestern U.S.; Mexico; Central America ..... 11
- Southern Florida; West Indies ..... 12
- 11(10). Ostiolar canal narrowed at middle, becoming slightly wider towards apex (Fig. 137); posterolateral angle of each abdominal sternite usually immaculate; apex of each paramere nearly spinose in medial view (Fig. 124) (southwestern U.S.; northwestern Mexico) ..... *planifrons* Ruckes
- Ostiolar canal acuminate apically; posterolateral angle of each abdominal sternite piceous, sometimes only a minute portion of the tip piceous; apex of each paramere narrowly rounded in medial view (Fig. 140) (southern Texas; Mexico; Central America) ..... *maculata* (Fabricius)
- 12(10). Each paramere in medial view with apex straight or bending slightly ventrad (Fig. 155), concave surface oriented more mediad than dorsad; posteromesial angles of basal plates distinctly excavated, resulting concavity broadly U-shaped (Fig. 165) (Trinidad and Tobago; Venezuela) ..... *vadora* Rider
- Each paramere in medial view with apex curving slightly dorsad, orientation of dorsomedial concave surface variable; posteromesial angles of basal plates rounded or weakly emarginate ..... 13
- 13(12). Concave surface of each paramere oriented more mediad than dorsad (southern Florida) ..... *pseudocasta* Blatchley
- Concave surface of each paramere oriented more dorsad than mediad ..... 14
- 14(13). Apex of each paramere rounded in ectal view (Fig. 186); spermathecal duct with relatively small amount of swelling and coiling below proximal flange (Fig. 197) (Greater Antilles) ..... *obsoleta* (Dallas)
- Apex of each paramere spinose in ectal view (Fig. 201); spermathecal duct with large amount of swelling and coiling below proximal flange, swelling carrot-shaped (Fig. 212) (Lesser Antilles; northern South America) ..... *testacea* (Dallas)

#### Subgenus *Thyanta* Stål

*Diagnosis.* Punctures minute, dense. Posterior terminations of bucculae evanescent. Anterolateral pronotal margins straight to concave, sometimes marked with piceous;

humeral angles rounded to angulate, often spinose; pronotal cicatrices sometimes marked with piceous in mesial angles. Ostiolar canals acuminate apically. Superior surface of each tibia sulcate.

Posterior margins of basal plates sinuous, posteromesial angles entire (Fig. 13). Distal end of sclerotized rod cone-shaped (Fig. 14); spermathecal bulb digitiform; cylindrical structure below proximal flange (Fig. 15). Pygophoral opening small, subtended on posteroventral surface by a rectangular or semicircular impression; posterior margin of pygophore straight to concave in caudal view, with medially incised protuberance in middle (Fig. 9). Each paramere F-shaped, obtuse protuberance on shaft usually prominent, apex spinose, ectal surface convex (Fig. 3), roughened spiculate area on lateral surface linear (Fig. 5). Each lateral conjunctival lobe of aedeagus with single spinose diverticulum (Fig. 6); dorsomedial conjunctival lobe usually well-developed (Fig. 7), theca large; subtriangular in lateral view, with dorsolateral protuberance on each side near caudal limit (Fig. 8); medial penial lobes and penisfilum moderate in size.

*Comments.* Species of the subgenus *Thyanta* have the pygophoral opening subtended by a semicircular or rectangular impression, and the posterior margin is distinctly emarginate medially. Species of *Phacidium* have the posteroventral surface of the pygophore arcuately rounded or sulcate, and the posterior margin is not emarginate medially. The posteroventral surface of the pygophore in species of *Argosoma* is produced into a blunt, chin-like protuberance. The ectal surface of each paramere is concave in *Argosoma* and convex in both *Phacidium* and *Thyanta*.

The female genitalia are also useful in separating species of *Thyanta* and *Phacidium*. In *Thyanta*, the distal end of the sclerotized rod is cone-shaped, and the spermathecal bulb is digitiform. In *Phacidium*, the distal end of the sclerotized rod is swollen subapically and narrowed distally, and the spermathecal bulb is globose. The female genitalia of both *Phacidium* and *Argosoma* are very similar, but females can usually be separated by dorsal punctuation which is relatively dense in *Phacidium* and less dense and more coarse in *Argosoma*.

*Thyanta (Thyanta) calceata* (Say)  
Figs. 1–15, Map 1

*Pentatoma calceata* Say, 1831:8.

*Thyanta custator* (of authors, not Fabricius): Herrich-Schäffer, 1844:96, 106, fig. 771; Uhler, 1886:7 (part); Lethierry and Severin, 1893:148 (part); Kirkaldy, 1909:94 (part); Banks, 1910:90 (part).

*Thyanta custator calceata*: Uhler, 1872:399.

*Thyanta calceata*: Barber, 1911:108–111; Van Duzee, 1917:53; Hart, 1919:184, 217, fig. 70; Blatchley, 1926:113, 117–118; Torre-Bueno, 1939:231; Ruckes, 1957a:21–22; Hoffman, 1971:44; Furth, 1974:22, 23–24; McPherson, 1982:76–77, 79–80, fig. 72; Rolston and McDonald, 1984:figs. 23, 27; Froeschner, 1988:593.

*Diagnosis.* General form broad, ovate. Transhumeral rubiginous band usually present; vertex of head and tylus often reddish.

Lateral jugal margins nearly parallel for middle third of distance from eyes to apex (Fig. 2). Humeral angles rounded to angulate; anterolateral pronotal margins piceous, straight to weakly concave in dorsal view (Fig. 1); mesial angle of each pronotal

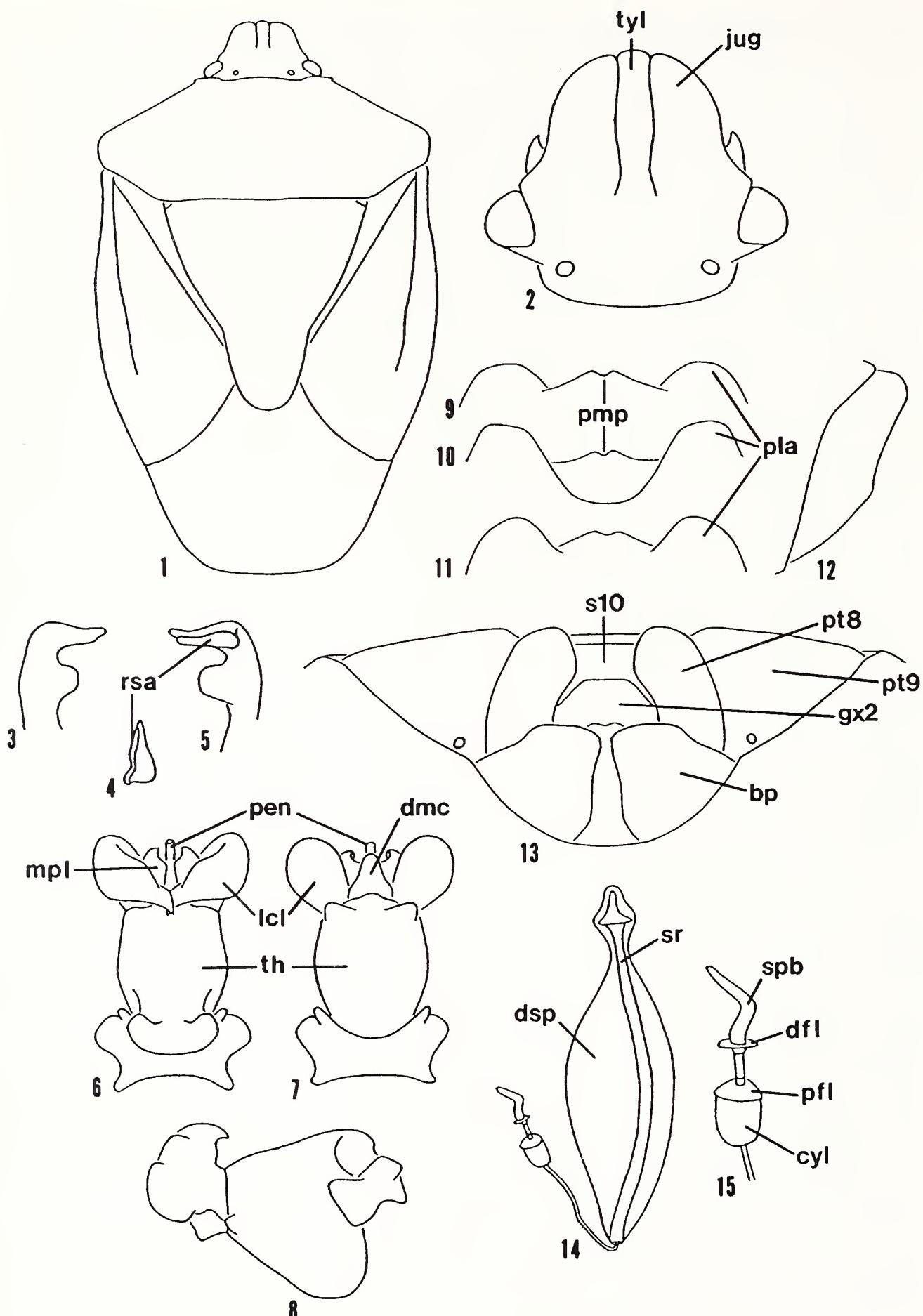
cicatrice piceous. Each abdominal sternite with postspiracular spot on each side and posterolateral angles piceous.

Mesial margins of basal plates in caudoventral view slightly concave; posterior margins sinuous; posteromesial angles rounded (Fig. 13). Posterolateral angles of pygophore continuing onto posteroventral surface as vague carinae, forming semi-circular impression in caudoventral view. Posterior margin of pygophore produced posterodorsad, in ventral and dorsal views appearing convex with small, medial, V-shaped emargination (Figs. 10, 11); slightly concave in lateral view (Fig. 12).

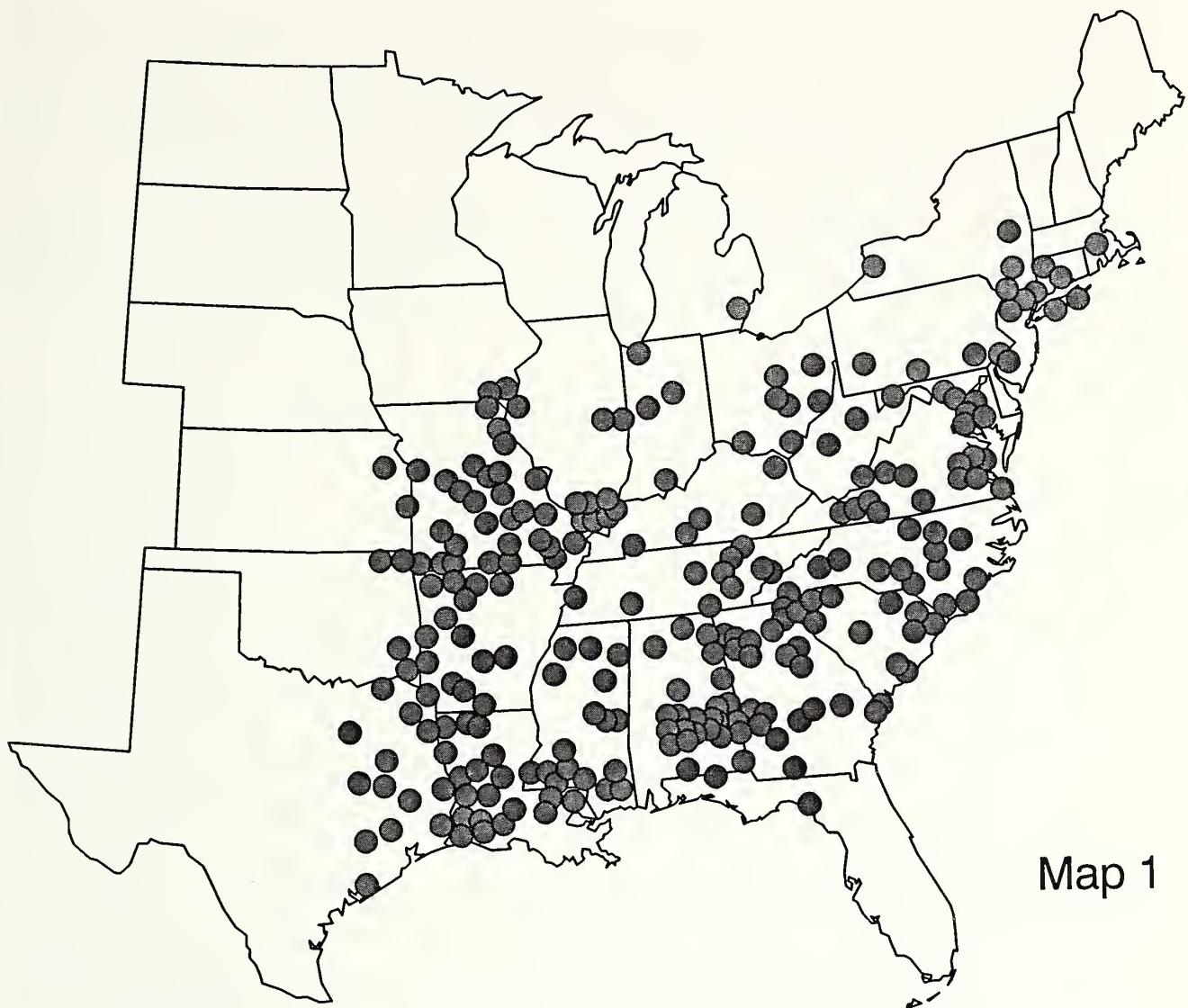
**Types.** The type specimen of *Pentatoma calceata* is apparently no longer in existence, and Say's original description (1831) will fit equally well for either *T. calceata* or *T. custator*. Previous usage has, however, fixed both species, and therefore designation of a neotype is not necessary.

**Distribution.** Eastern U.S. (Map 1).

**Specimens examined.** 1,105 specimens collected during every months of the year; deposited in AMNH, ARH, AUA, CAS, CNC, CUC, DAR, DBT, EGER, FMNH, FSCA, INHS, ISU, LRH, LSU, MSU, MSUE, NCSU, NDSF, OSUC, POLH, PUL, SIUC, SMEK, TAMU, UAT, UCB, UCR, UCS, UGA, UIM, UMC, USNM, VPI, WSU. UNITED STATES: Alabama: Autauga, Barbour, Bibb, Cherokee, Chilton, Clay, Cleburne, Coosa, Covington, Dallas, De Kalb, Elmore, Houston, Lee, Lowndes, Macon, Madison, Perry, Randolph, Shelby, Tallapoosa, Wilcox, Winston. Arkansas: Benton, Boone, Carroll, Grant, Hempstead, Hot Spring, Logan, Marion, Nevada, Newton, Polk, Sevier, Union, Yell. Connecticut: Litchfield, New Haven. District of Columbia. Florida: Collier, Holmes, Taylor. Georgia: Bartow, Bibb, Bryan, Chatham, Clark, Cobb, De Kalb, Floyd, Franklin, Fulton, Habersham, Hall, Harris, Johnson, Madison, Marion, Oconee, Oglethorpe, Paulding, Peach, Rabun, Sumter, Talbot, Thomas. Illinois: Champaign, Franklin, Hancock, Hardin, Jackson, Johnson, Pope, Union, Vermilion, Williamson. Indiana: Crawford, Howard, Porter, Tippecanoe. Iowa: Henry, Van Buren. Kansas: Bourbon, Douglas. Kentucky: Barren, Carter, Green, Laurel, Trigg. Louisiana: Allen, Acadia, Beauregard, Caddo, Calcasieu, Claiborne, De Soto, East Baton Rouge, East Feliciana, Grant, Jefferson Davis, Natchitoches, Rapides, Sabine, St. Landry, Tangipahoa, Vernon, Webster, West Feliciana, Winn. Maryland: Allegany, Anne Arundel, Calvert, Charles, Frederick, Montgomery, Prince Georges. Massachusetts: Bristol. Michigan: Wayne. Mississippi: Adams, Amite, Copiah, Forrest, Franklin, Jones, Lauderdale, Leake, Lincoln, Monroe, Newton, Oktibeha, Panola, Perry, Pontotoc, Tallahatchie, Walthal. Missouri: Barry, Benton, Boone, Butler, Callaway, Camden, Carter, Crawford, Dade, Douglas, Greene, Harrison, Jackson, Laclede, Marion, McDonald, Montgomery, Osage, Ozark, Pettis, Phelps, Ralls, Randolph, St. Charles, St. Francois, Scotland, Scott, Shannon, Stone, Taney, Wright. New Jersey: Bergen, Gloucester, Morris. New York: Albany, Erie, Nassau, Orange, Suffolk, Ulster, Westchester. North Carolina: Buncombe, Columbus, Craven, Cumberland, Currituck, Harnett, Johnston, McDowell, Macon, Montgomery, Moore, Orange, Pender, Scotland, Wake. Ohio: Adams, Fairfield, Gallia, Hocking, Licking, Pickaway, Tuscarawas, Washington. Oklahoma: Craig, Latimer, McCurtain, Ottawa. Pennsylvania: Franklin, Lancaster, Philadelphia, Westmorland. South Carolina: Abbeville, Charleston, Chesterfield, Dorchester, Florence, Greenville, Horry, Lexington, Oconee, Pickens, Spartanburg, Williamsburg. Tennessee: Cumberland, Decatur, De Kalb, Fentress, Knox, Lauderdale, Marion, Rhea, Scott, Sevier. Texas: Anderson,



Figs. 1–15. *T. calceata*. 1. Habitus. 2. Head. 3–5. Right paramere. 3. Medial view. 4. Ectal view. 5. Lateral view. 6–8. Theca and related structures. 6. Ventral view. 7. Dorsal view. 8. Lateral view. 9–12. Pygophore. 9. Caudal view. 10. Ventral view. 11. Dorsal view. 12. Lateral



Map 1

Map 1. *T. calceata*.

*Angelina, Aransas, Bowie, Brazos, Camp, Cherokee, Dallas, Harris, Harrison, Jasper, Lamar, Sabine, Smith, Walker. Virginia: Charolette, Chesterfield, Clifton Forge City, Fairfax, Falls Church, Floyd, Gloucester, Hanover, King & Queen, Montgomery, Nelson, New Kent, Norfolk, Pulaski, Virginia Beach, Wythe. West Virginia: Monroe, Roane, Upshur.*

*Comments.* *Thyanta calceata* can be separated from all other congeners except *T. custator custator* by the distinctly black anterolateral pronotal margins. It can be reliably distinguished from *T. c. custator* only by the male genitalia. In *T. calceata*, the pygophoral opening is subtended by a semicircular impression; this impression

↑ view. 13. Genital plates, caudoventral view. 14. Spermatheca. 15. Spermathecal pump. Symbols: bp, basal plate; cyl, cylindrical structure below proximal flange; dfl, distal flange; dmc, dorso-medial conjunctival lobe; dsp, dilation of spermatheca; gx2, second gonacoxae; jug, juga; lcl, lateral conjunctival lobe; mpl, median penial lobe; pen, penisfilum; pfl, proximal flange; pla, posterolateral angle of pygophore; pmp, posterior margin of pygophore; pt8, eighth paratergite; pt9, ninth paratergite; rsa, roughened spiculate area on lateral surface of paramere; spb, spermathecal bulb; sr, sclerotized rod; s10, tenth sternite; th, theca; tyl, tylus.

is rectangular in *T. c. custator*. Specimens of *T. calceata* are generally shorter and broader than specimens of *T. c. custator*, and the black markings on the anterolateral pronotal margins are usually darker and more extensive in *T. calceata*. These last two characters, however, may be apparent only when a series of specimens of each species can be compared.

Most species of *Thyanta* occur in two color forms, a green form in the warmer months and a brown form in the cooler months. This is particularly well documented in *T. calceata* (McPherson, 1977a, b, 1978a, b; McPherson and Paskewitz, 1982; McPherson et al., 1983).

*Thyanta (Thyanta) custator custator* (Fabricius)

Figs. 16–30, Map 2

*Cimex custator* Fabricius, 1803:164.

*Pentatoma custator*: Dallas, 1851:251; Walker, 1867:288.

*Thyanta custator*: Stål, 1862a:58; Stål, 1872:34–35 (part); Uhler, 1872:399 (part); Uhler, 1876:289–290 (part); Uhler, 1886:7 (part); Van Duzee, 1904:53 (part); Kirkaldy, 1909:94 (part); Van Duzee, 1909:155–156; Banks, 1910:90 (part); Barber, 1911:108–111 (part); Barber, 1914:523; Van Duzee, 1917:52 (part); Blatchley, 1926:113, 115–116 (part); Torre-Bueno, 1939:231 (part); Ruckes, 1957a:1–2, 4–13, 20, 22, fig. 1; Ueshima, 1963:149, 152–153; Hoffman, 1971:44–45; Furth, 1974:22, 23, fig. 45; McPherson, 1982:76–77, 80–81, fig. 73; Rolston and McDonald, 1984:figs. 24, 28; Froeschner, 1988:593.

*Thyanta accerra* (of authors, not McAtee): Blatchley, 1926:114, 118.

*Thyanta casta* (of authors, not Stål): Blatchley, 1926:113, 116–117.

*Diagnosis.* Dorsal surface green to brown, often with varying amount of reddish coloration between humeral angles, sometimes extending along anterolateral pronotal margins and onto basal margin of each corium.

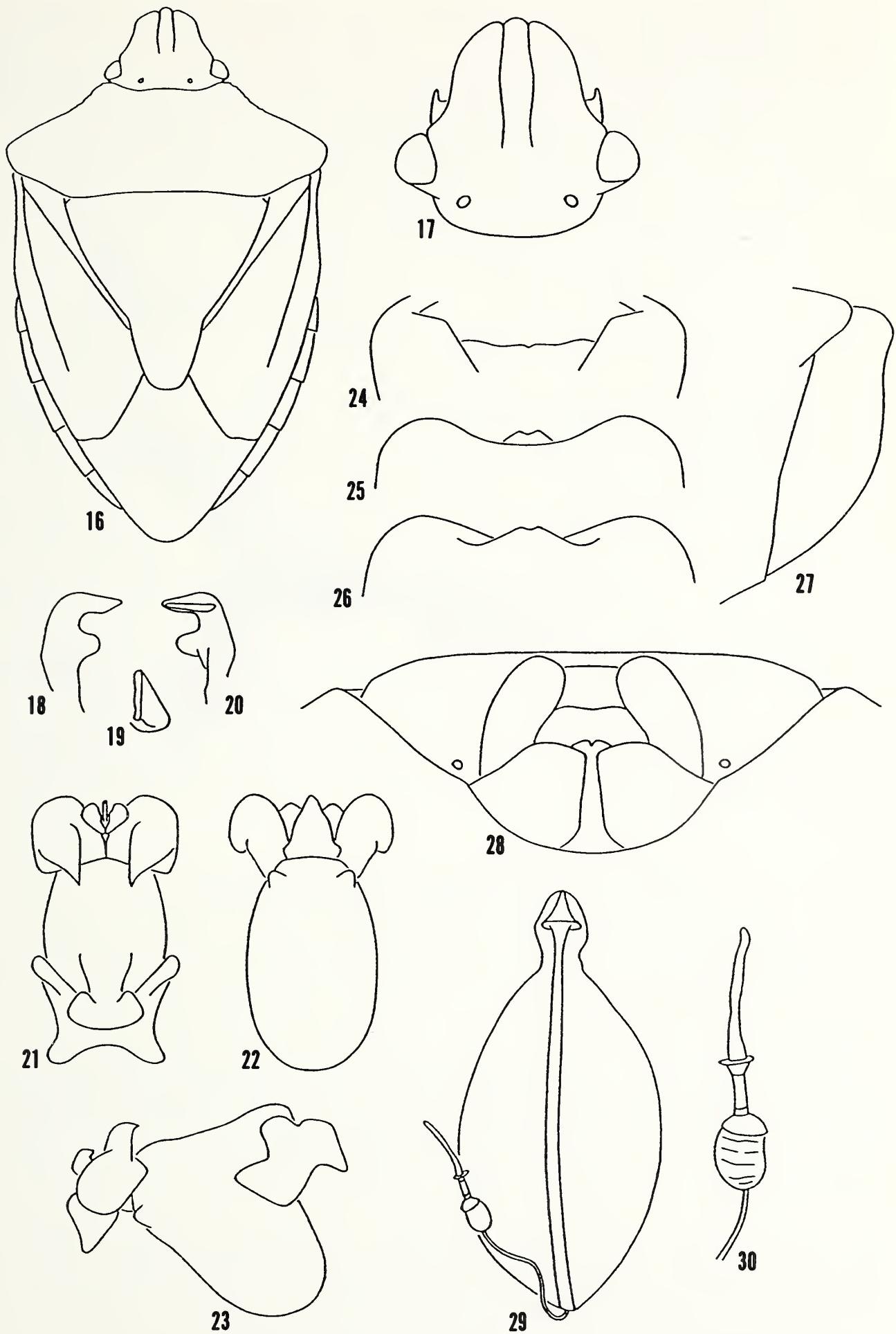
Lateral jugal margins sinuous, not parallel (Fig. 17). Anterolateral margins of pronotum and mesial angle of each pronotal cicatrice piceous. Anterolateral pronotal margins slightly concave in dorsal view; humeral angles rounded to angulate, never spinose (Fig. 16). Ventral surface yellow-green to brown, posterolateral angles of abdominal sternites black. Each abdominal sternite with postspiracular black spot on each side.

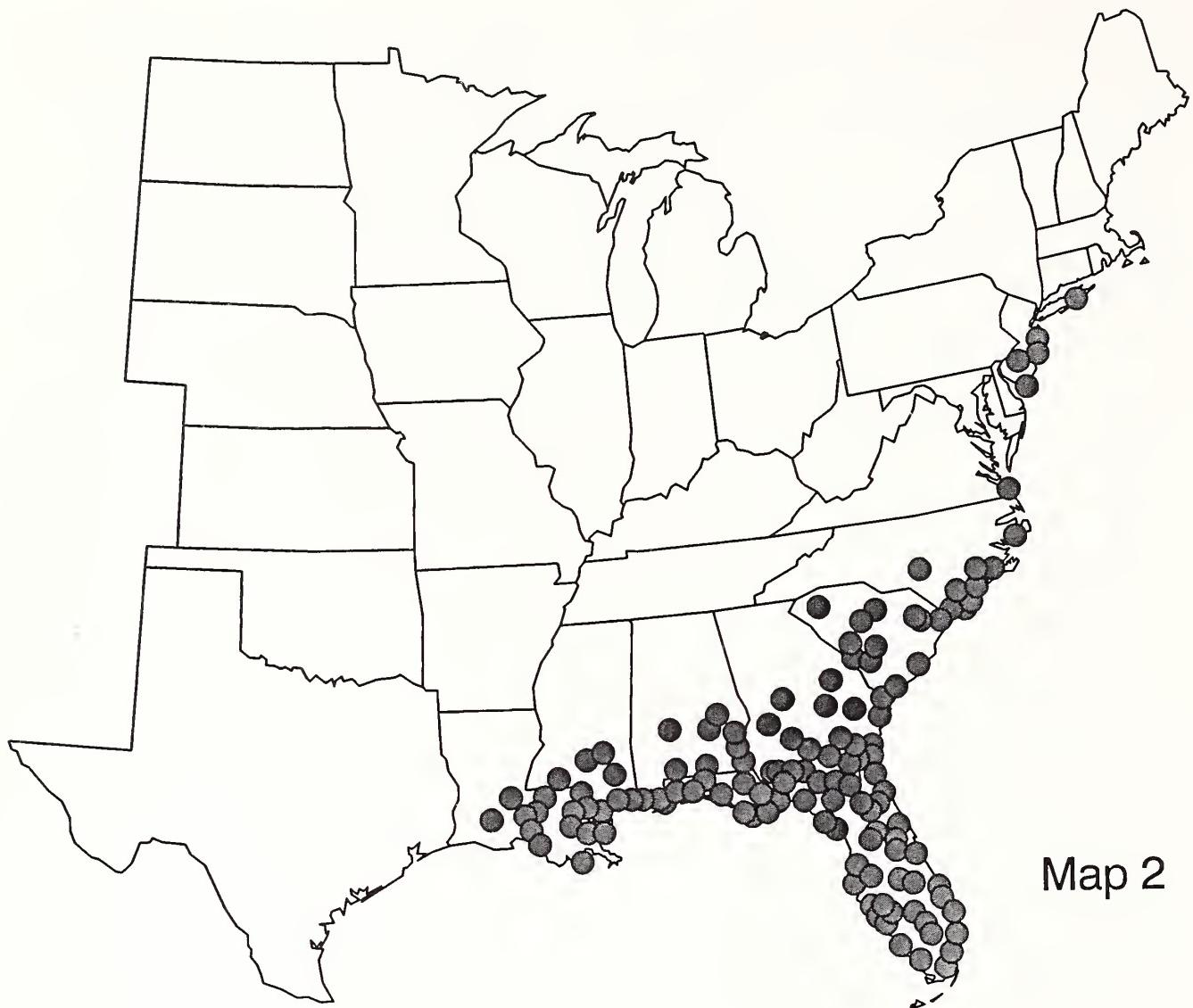
Mesial margins of basal plates nearly straight in caudoventral view; posterior margins sinuous; posteromesial angles narrowly rounded (Fig. 28). Each posterolateral angle of pygophore continuing onto posteroventral surface as vague carina, forming rectangular impression; mesial portion of posterior margin slightly convex with small, V-shaped, emargination in middle in both ventral and dorsal views (Figs. 25, 26); pygophore slightly concave in lateral view (Fig. 27).

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Figs. 16–30. *T. custator custator*. 16. Habitus. 17. Head. 18–20. Right paramere. 18. Medial view. 19. Ectal view. 20. Lateral view. 21–23. Theca and related structures. 21. Ventral view. 22. Dorsal view. 23. Lateral view. 24–27. Pygophore. 24. Caudal view. 25. Ventral view. 26. Dorsal view. 27. Lateral view. 28. Genital plates, caudoventral view. 29. Spermatheca. 30. Spermathecal pump.





Map 2. *T. custator custator*.

**Types.** The type specimen of *Cimex custator* is apparently no longer in existence (Zimsen, 1964), and the original description does not adequately fix the species. Fabricius' description will fit either *T. custator custator* and *T. calceata* equally well. Previous usage, however, has fixed both species, and therefore the designation of a neotype is not necessary.

**Distribution.** Coastal plain from central Louisiana to Florida to New York, and the Bahama Islands (Map 2).

**Specimens examined.** 1,243 specimens collected during every month of the year; deposited in AMNH, ARH, AUA, BMNH, CAS, CNC, CUC, DAR, DBT, FMNH, FSCA, INHS, ISU, LHR, LSU, MSU, MSUE, NCSU, OSUC, PUL, SIUC, SMEK, TAMU, UAT, UCB, UCR, UCS, UGA, UIM, UMC, USNM, UUSL, WSU. UNITED STATES: Alabama: Baldwin, Barbour, Covington, Dallas, Escambia, Henry, Houston, Lee, Macon, Madison, Mobile. Florida: Alachua, Bay, Brevard, Broward, Charlotte, Clay, Collier, Columbia, Dade, De Soto, Dixie, Duvall, Franklin, Gadsden, Glades, Gulf, Hamilton, Hardee, Hendry, Highlands, Hillsborough, Holmes, Indian River, Jackson, Lake, Lee, Leon, Levy, Liberty, Madison, Manatee, Marion, Martin, Nassau, Okaloosa, Orange, Osceola, Palm Beach, Pasco, Pinellas, Polk, Putnam, St. Johns, St. Lucie, Santa Rosa, Sarasota, Seminole, Sumter, Suwanee, Taylor, Volusia,

*Wakulla, Washington, Georgia: Berrien, Brantley, Brooks, Charlton, Chatham, Clinch, Decatur, Evans, Glynn, Grady, Jefferson, McIntosh, Peach, Pierce, Sumter, Thomas, Tifton, Toombs, Ware.* Louisiana: *Acadia, Ascension, Avoyelles, East Baton Rouge, East Feliciana, Iberville, Jefferson, Livingston, Orleans, St. Charles, St. James, St. Mary, St. Tammany, Tangipahoa, Washington, West Baton Rouge.* Mississippi: *Covington, Forrest, Hancock, Harrison, Jackson, Jefferson Davis, Pike.* New Jersey: *Burlington, Cape May, Monmouth, Ocean.* New York: *Suffolk.* North Carolina: *Bladen, Brunswick, Columbus, Duplin, Hyde, Moore, New Hanover, Onslow, Pender.* South Carolina: *Aiken, Bamberg, Barnwell, Beaufort, Charleston, Florence, Greenville, Horry, Jasper, Kershaw, Marion, Orangeburg, Richland.* Virginia: *Norfolk.* Bahama Islands: *South Bimini Island.*

*Comments.* This species has been the subject of much confusion in the past. At one time the name *T. custator* was applied to nearly all specimens from the entire United States. Ruckes (1957a) showed that the true *custator* form is confined to the coastal plain from Louisiana to Florida to New York, but he felt that it was a separate species distinct from the *accerra* form. The two forms have virtually identical genitalia. They cross-breed readily in the laboratory; and where their distributions overlap, specimens intermediate between the two forms are found fairly frequently. The two forms have a very narrow overlap in their respective ranges, however, and specimens taken from outside the area of overlap are usually easily identified. These two forms probably are more correctly considered subspecies.

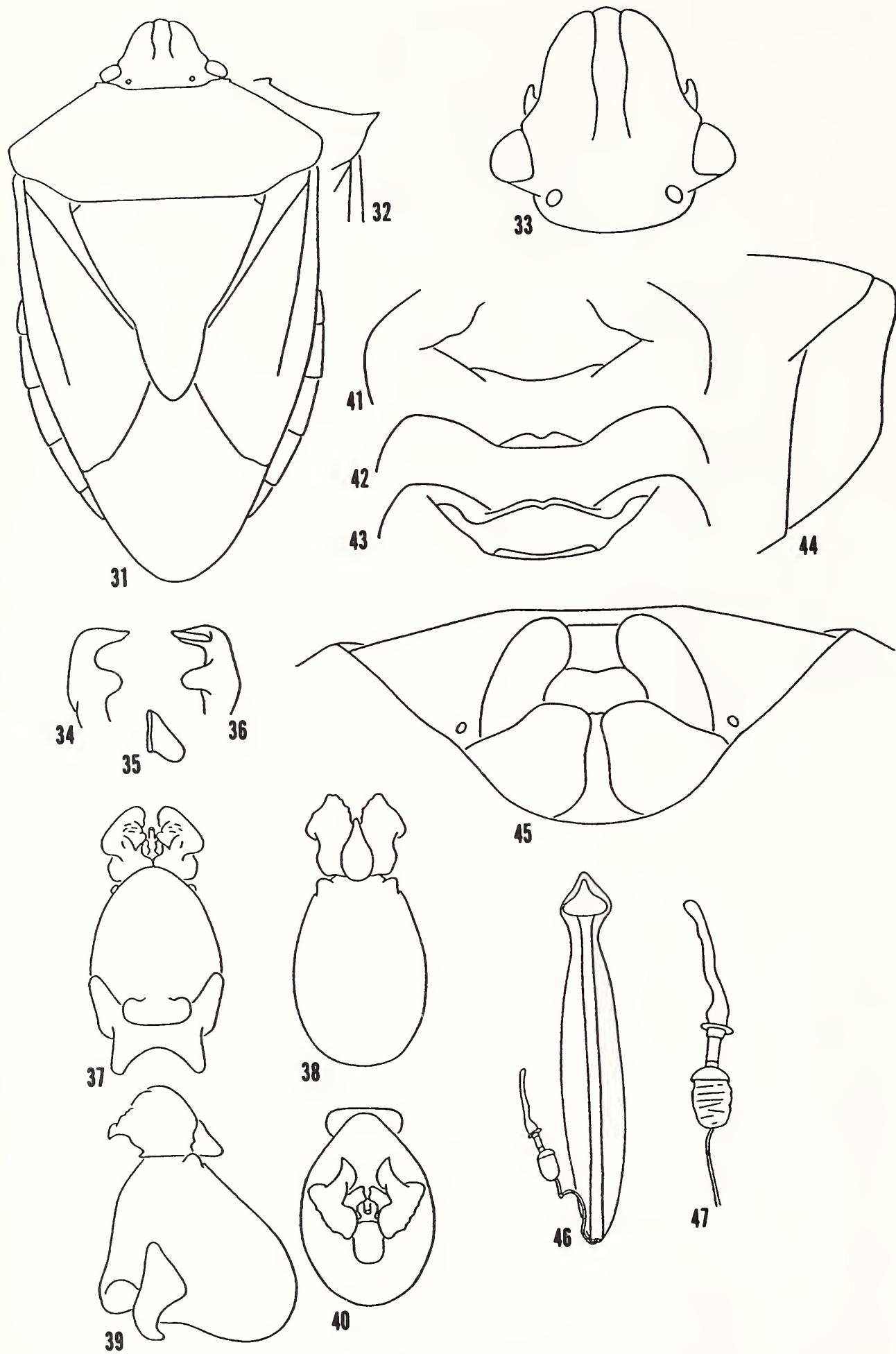
*Thyanta c. custator* and *T. calceata* are the only two species in the genus with distinctly black anterolateral pronotal margins. They can be separated reliably from each other only by the characters of the male genitalia. The pygophoral opening in *T. c. custator* is subtended by a rectangular impression, while this impression is semicircular in *T. calceata*. When large series are present, some separation can be made based on the general shape of the body: *T. custator* is slightly longer and narrower than *T. calceata*. Fortunately, there is very little overlap in their distributions.

*Thyanta (Thyanta) custator accerra McAtee*  
Figs. 31–47, Map 3

*Thyanta custator* var. *accerra* McAtee, 1919:16.

*Thyanta custator*: Stål, 1872:34–35 (part); Uhler, 1872:399 (part); Uhler, 1876:289–290 (part); Uhler, 1877:404; Popenoe, 1884:62; Uhler, 1886:7 (part); Lethierry and Severin, 1893:148 (part); Osborn, 1894:121; Uhler, 1894a:230–231; Van Duzee, 1894:171; Blatchley, 1895:269; Gillette and Baker, 1895:16; Van Duzee, 1904:53 (part); Barber, 1906:260; Kirkaldy, 1909:94 (part); Banks, 1910:90 (part); Barber, 1911:108–111 (part); Zimmer, 1912:232–233; Torre-Bueno, 1914:92; Van Duzee, 1914:4–5 (part); Van Duzee, 1917:52 (part); Hart, 1919:184–185; Malloch, 1919:217, fig. 75; Blatchley, 1926:113, 115–116 (part); Torre-Bueno, 1939:231 (part).

*Thyanta perditor* (of authors, not Fabricius): Uhler, 1872:399 (part); Uhler, 1876:289 (part); Uhler, 1877:404 (part); Popenoe, 1884:62; Uhler, 1886:7; Osborn, 1894:121; Uhler, 1894a:230 (part); Gillette and Baker, 1895:16; Van Duzee, 1904:52–53 (part); Kirkaldy, 1909:95 (part); Zimmer, 1911:232 (part); Torre-Bueno, 1914:92; Malloch, 1919:217, fig. 79; Blatchley, 1926:113, 114–115, fig. 24 (part).



*Thyanta pallido-virens* (of authors, not Stål): Banks, 1910:90 (part); Rolston and McDonald, 1984:fig. 31.

*Thyanta accerra*: Deay and Gould, 1935:305–306; Torre-Bueno, 1939:233; Harris, 1943:150; Ward et al., 1977:40; McPherson, 1979b:94; McPherson, 1982:77, 78–79, fig. 167; Froeschner, 1988:592–593.

*Thyanta pallidovirens accerra*: Ruckes, 1957a:14–15, 19–22; Ueshima, 1963:152–153; Hoffman, 1971:44–45; Furth, 1974:22–23; McPherson, 1979a:83–84.

*Thyanta pallidovirens spinosa* Ruckes, 1957a:18–19; Ward et al. 1977:40; Froeschner, 1988:593. **NEW SYNONYMY.**

*Diagnosis.* Green to dark brown, sometimes with varying amounts of reddish coloration between humeral angles, often extending onto basal margin of each corium.

Lateral jugal margins sinuous, not parallel (Fig. 33). Humeral angles rounded to angulate (spinose in desert areas of southwestern United States and Mexico); anterolateral margins of pronotum straight to concave in dorsal view (Figs. 31, 32), stramineous to green, sometimes reddish, but never piceous; pronotal cicatrices immaculate. Each abdominal sternite with postspiracular black spot present on each side (eastern U.S.) or absent (western U.S.). Posterolateral angles of abdominal sternites immaculate or minutely marked with piceous.

Mesial margins of basal plates in caudoventral view slightly concave; posterior margins sinuous; posteromesial angles rounded (Fig. 45). Posterolateral angles of pygophore continuing onto posteroventral surface of pygophore as vague carinae, forming rectangular impression; mesial portion of posterior margin of pygophore convex with slight mesial emargination in ventral and dorsal views (Figs. 42, 43); pygophore only slightly concave in lateral view (Fig. 44).

*Types.* McAtee (1919) described *accerra* as a variety of *T. custator*; he examined four specimens: three from Barachias, Alabama, and one from San Antonio, Texas. Blatchley (1926) elevated *accerra* to full species rank, but his concept of the species was incorrect. Blatchley's *T. accerra* was actually *T. c. custator*. The type specimens, which are housed in the U.S. National Museum of Natural History (Washington, D.C.), were examined.

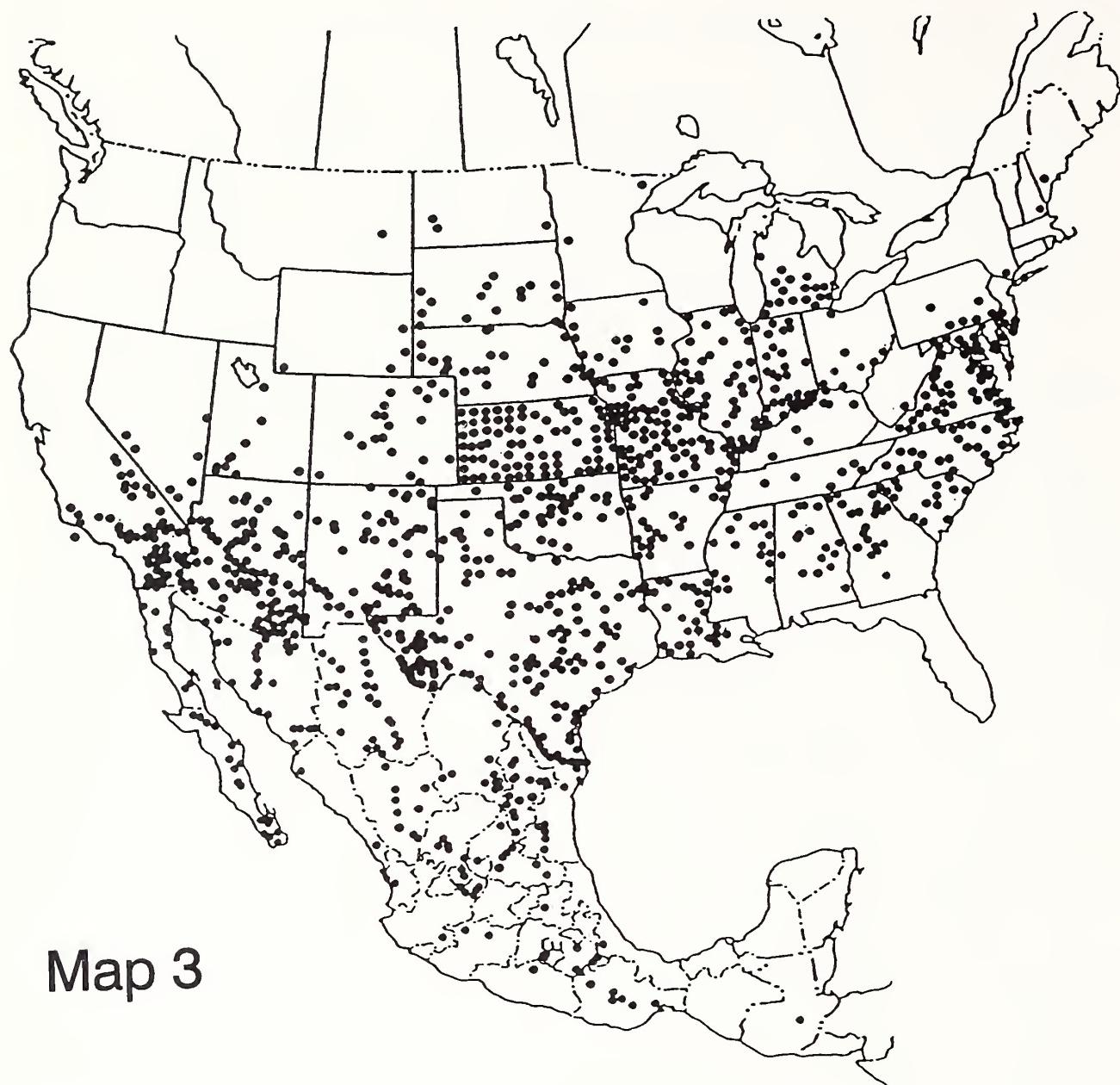
Ruckes (1957a) described *T. pallidovirens spinosa* from 75♂♂ and 51♀♀ specimens. The holotype, which was examined, is from Patagonia, Santa Cruz Co., Arizona, and is deposited in the American Museum of Natural History (New York).

*Distribution.* Eastern two-thirds of U.S. west to Montana, Nevada, and southern California; Mexico; and Guatemala (Map 3).

*Specimens examined.* 8,677 specimens collected during every month of the year; deposited in AMNH, ARH, ASUT, AUA, BMNH, CAS, CNC, CUC, DAR, DBT, EGER, ENGL, FMNH, FSCA, INHS, ISU, LACM, LHR, LSU, MSU, MSUB, MSUE, NCSU, NDSF, NMSU, OSUC, POLH, PUL, SIUC, SMEK, TAMU, UAT,

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←  
Figs. 31–47. *T. custator accerra*. 31. Habitus. 32. Variation in humeral angle. 33. Head. 34–36. Right paramere. 34. Medial view. 35. Ectal view. 36. Lateral view. 37–40. Theca and related structures. 37. Ventral view. 38. Dorsal view. 39. Lateral view. 40. Ectal view. 41–44. Pygophore. 41. Caudal view. 42. Ventral view. 43. Dorsal view. 44. Lateral view. 45. Genital plates, caudoventral view. 46. Spermatheca. 47. Spermathecal pump.



Map 3

Map 3. *T. custator accerra*.

UCB, UCR, UCS, UGA, UIM, UMAA, UMC, UNAM, UNL, USNM, UUSL, VPI, WSU. UNITED STATES: Alabama: *Chambers, Dallas, De Kalb, Elmore, Green, Henry, Jefferson, Lee, Macon, Madison, Montgomery, Morgan, St. Clair, Tallapoosa*. Arizona: *Apache, Cochise, Coconino, Gila, Graham, Greenlee, Maricopa, Mohave, Navajo, Pima, Pinal, Santa Cruz, Yavapai, Yuma*. Arkansas: *Benton, Boone, Conway, Graighead, Faulkner, Garland, Hempstead, Hot Spring, Howard, Lawrence, Lincoln, Little River, Logan, Mississippi, Montgomery, Newton, Pike, Polk, Pulaski, Washington, Yell*. California: *Imperial, Inyo, Kern, Los Angeles, Riverside, San Bernardino, San Diego, Santa Barbara, Ventura*. Colorado: *Boulder, Chafee, Clear Creek, Douglas, El Paso, Jefferson, Gunnison, Larimer, Las Animas, Lincoln, Logan, Montezuma, Morgan, Otero, Prowers, Pueblo, Teller, Washington, Yuma*. Delaware: Kent. District of Columbia. Florida: *Highlands*. Georgia: *Bartow, Clarke, Crawford, Dade, Decatur, Fulton, Habersham, Henry, Lamar, Macon, Madison, Morgan, Oconee, Oglethorpe, Peach, Spalding, Talbot, Twiggs, Whitfield, Wilkes, Worth*. Hawaii: *Honolulu*. Illi-

nois: Adams, Alexander, Cass, Champaign, Clay, Coles, Cook, Cumberland, Edgar, Effingham, Grundy, Hancock, Hardin, Henry, Jackson, Jo Daviess, Johnson, Kankakee, Macon, Macoupin, Madison, Marion, Marshall, Mason, Massac, McDonough, McHenry, Menard, Morgan, Ogle, Peoria, Piatt, Pope, Pulaski, St. Clair, Scott, Union, Vermilion, Wabash, Warren, Washington, White, Will, Williamson. Indiana: Cass, Clark, Dearborn, Floyd, Greene, Harrison, Howard, Jackson, Jefferson, Jennings, Johnson, Knox, Kosciusko, Lagrange, Lake, Lawrence, Marion, Morgan, Noble, Owen, Parke, Perry, Posey, Putnam, St. Joseph, Starke, Switzerland, Tippecanoe, Vanderburgh, Washington, Wayne. Iowa: Audubon, Boone, Floyd, Fremont, Harrison, Johnson, Linn, Lyon, Monona, Polk, Story, Union, Woodbury. Kansas: Allen, Anderson, Atchison, Barbor, Bourbon, Chautauqua, Cherokee, Cheyenne, Clark, Comanche, Decatur, Dickenson, Doniphan, Douglas, Ellis, Ellsworth, Finney, Ford, Geary, Gove, Graham, Gray, Greeley, Greenwood, Hamilton, Harper, Harvey, Hodgeman, Johnson, Kearny, Kingman, Kiowa, Labette, Lane, Leavenworth, Linn, Logan, Meade, Miami, Mitchell, Montgomery, Morton, Neosho, Norton, Osborne, Ottawa, Pawnee, Phillips, Pottawatomie, Pratt, Rawlins, Reno, Riley, Rooks, Rush, Russell, Scott, Sedgwick, Seward, Sheridan, Sherman, Smith, Stafford, Stanton, Stevens, Sumner, Thomas, Wabaunsee, Wallace, Washington, Wichita, Wilson. Kentucky: Campbell, Christian, Fayette, Green, Hardin, Jefferson, Oldham, Rowan, Scott, Trimble. Louisiana: Acadia, Avoyelles, Bossier, Caddo, Calcasieu, Cameron, Catahoula, Claiborne, Concordia, East Baton Rouge, East Feliciana, Evangeline, Franklin, Grant, Iberville, Jefferson Davis, Livingston, Madison, Natchitoches, Ouachita, Rapides, Richland, St. Landry, Tensas, Vermilion, Webster, West Baton Rouge. Maine: Oxford. Maryland: Allegany, Anne Arundel, Baltimore, Calvert, Frederick, Montgomery, Prince Georges, Queen Annes, Talbot, Washington. Michigan: Barry, Berrien, Calhoun, Ingham, Ionia, Jackson, Kalamazoo, Kent, Lenawee, Livingston, Mason, Montcalm, Oakland, Shiawassee, Van Buren, Washtenaw, Wayne. Minnesota: Grant, St. Louis. Mississippi: Bolivar, Clay, Grenada, Hinds, Issaquena, Lauderdale, Lee, Lowndes, Marshall, Monroe, Noxubee, Oktibbeha, Panola, Pontotoc, Warren, Yazoo. Missouri: Atchison, Audrain, Barry, Barton, Benton, Boone, Buchanan, Caldwell, Callaway, Camden, Cape Girardeau, Carroll, Carter, Cedar, Chariton, Clark, Clay, Clinton, Cole, Cooper, Crawford, Dade, Dallas, Douglas, Dunklin, Franklin, Gasconade, Gentry, Greene, Grundy, Henry, Howard, Howell, Jackson, Jasper, Johnson, Lafayette, Lawrence, Lewis, Lincoln, Livingston, Madison, Maries, Marion, Miller, Mississippi, Moniteau, Montgomery, Morgan, New Madrid, Newton, Nodaway, Oregon, Osage, Pemiscot, Pettis, Phelps, Pike, Platte, Polk, Putnam, Ralls, Rankin, Ray, Reynolds, St. Charles, Ste. Genevieve, St. Louis, Saline, Scott, Shannon, Stoddard, Stone, Sullivan, Taney, Vernon, Warren, Washington, Wright. Montana: Custer. Nebraska: Adams, Cass, Chase, Cherry, Cheyenne, Custer, Frontier, Garden, Hall, Keith, Lancaster, Lincoln, Morrill, Nance, Otoe, Scotts Bluff, Sioux, Thomas, Thurston. Nevada: Clark, Esmeralda, Lincoln, Mineral, White Pine. New Hampshire: Rockingham. New Jersey: Atlantic, Burlington, Cape May, Cumberland, Gloucester, Salem. New Mexico: Bernalillo, Catron, Chaves, Cibola, Colfax, De Baca, Dona Ana, Eddy, Grant, Guadalupe, Hidalgo, Lincoln, Luna, McKinley, Otero, Quay, Rio Arriba, Roosevelt, Sandoval, San Miguel, Santa Fe, Torrance, Union, Valencia. New York: Orange. North Carolina: Bertie, Bladen, Caldwell, Chowan, Cleveland, Craven, Dare, Duplin, Edgecombe, Granville, Iredell, Johnston, McDowell, Mecklenberg, Montgomery, Moore,

*Pasquotauk, Pender, Person, Rowan, Scotland, Vance, Wake, Warren, Washington, Wayne.* North Dakota: *Cass, Hettinger, Stark.* Ohio: *Adams, Athens, Clinton, Franklin, Hamilton, Lawrence, Lucas, Monroe, Pickaway, Sandusky, Trumbull, Washington.* Oklahoma: *Alfalfa, Beckham, Caddo, Canadian, Carter, Cleveland, Comanche, Custer, Garfield, Grant, Harper, Jackson, Kay, Kingfisher, Lincoln, Logan, Mayes, McIntosh, Noble, Oklahoma, Osage, Pawnee, Payne, Sequoyah, Stephens, Texas, Tulsa, Wagoner, Woods, Woodward.* Pennsylvania: *Adams, Berks, Bucks, Centre, Franklin, Lancaster.* South Carolina: *Abbeville, Allendale, Anderson, Barnwell, Charleston, Chesterfield, Florence, Horry, Laurens, Lee, Marlboro, Oconee, Richland, Spartanburg, Sumter.* South Dakota: *Beadle, Bennett, Brookings, Brule, Buffalo, Clay, Custer, Fall River, Jones, Lawrence, Minnehaha, Pennington, Stanley, Sully, Tripp, Union.* Tennessee: *Benton, Cooke, Davidson, Hamilton, Knox, Roane, Sevier.* Texas: *Anderson, Aransas, Atascosa, Bailey, Bandera, Bastrop, Bee, Bell, Bexar, Bosque, Brazos, Brewster, Burleson, Burnet, Caldwell, Cameron, Camp, Collin, Colorado, Comal, Comanche, Coryell, Crockett, Crosby, Culberson, Dallas, Deaf Smith, Denton, Dimmit, Donley, Duval, Eastland, El Paso, Erath, Fayette, Flatonia, Floyd, Frio, Galveston, Gillespie, Gonzales, Gray, Guadalupe, Hale, Harris, Hays, Hemphill, Hudspeth, Hill, Houston, Howard, Jackson, Jeff Davis, Jim Hogg, Jim Wells, Kaufman, Kendall, Kennedy, Kerr, Kimble, King, Kinney, Kleberg, Knox, Leon, Live Oak, Llano, Lubbock, Lynn, Madison, Marion, Maverick, McLennon, Medina, Milam, Montague, Moore, Motley, Nueces, Oldham, Palo Pinto, Parker, Pecos, Potter, Presidio, Randall, Real, Reeves, Robertson, Runnels, San Patricio, Shelby, Smith, Starr, Sutton, Swisher, Tarrant, Taylor, Terrell, Travis, Upshur, Uvalde, Val Verde, Victoria, Walker, Ward, Webb, Wichita, Willbarger, Willacy, Williamson, Wise, Zapata.* Utah: *Iron, Juab, Kane, Piute, Salt Lake, Sanpete, Sevier, Washington.* Virginia: *Accomack, Albemarle, Appamattox, Arlington, Augusta, Bedford, Buckingham, Campbell, Caroline, Carroll, Charlotte, Charlottesville City, Chesterfield, Clifton Forge City, Frederick, Hampton, James City, King George, King William, Loudoun, Montgomery, Nelson, New Kent, Newport News City, Norfolk City, Patrick, Pittsylvania, Petersburg City, Prince Edward, Richmond City, Roanoke, Rockbridge, Rockingham, Staunton City, Suffolk, Virginia Beach City, Westmorland, Winchester City, Wythe.* West Virginia: *Monroe, Morgan.* Wisconsin. Wyoming: *Goshen, Laramie, Niobrara, Uinta.*

MÉXICO: *Aguascalientes: Aguascalientes; Arroyo San Pedro, 38 mi N Aguascalientes. Baja California Norte: Bahía de los Angeles; Canyon del Tajo; Diablo Dry Lake, San Felipe Valley; Ensenada; Gonzaga Bay; Guadelupe Canyon; 4 mi SW La Zopopita; L Cantillas Canyon; 60 mi S Mexicali; Mission San Borja; Persebu; 13 mi S Puertocitos; 24 mi N Punta Prieta; 9 mi SE Rancho Laguna Chapola; 7 mi NE Ranch Rosarito; San Felipe; 15 mi S San Felipe; 21 km S San Quintin. Baja California Sur: Bahía Concepción; 40 mi S El Arco Mine; La Paz; 7 mi SW La Paz; 25 mi W La Paz; Las Tinajitas; Loreto; 10.3 mi SW Los Mendanos; 8 mi SW Mission San Javier; 15 mi N San Ignacio; San José de Comondu; 4 mi W San José del Cabo; 5 mi SE Santa Rosalía; 10 mi W Santa Rosalía; Santiago; 1 mi E Todos Santos; 4 mi N Todos Santos; 30 mi E V. Insurgentes; 45.5 mi E V. Insurgentes. Chiapas: Cintalpa; Comitán. Chihuahua: Ciudad Camargo; 20 mi SW Ciudad Camargo; 25 mi SW Ciudad Camargo; Catarinas; Chihuahua; 3 mi NW Chihuahua; 16 mi SE Chihuahua; 46 mi N Chihuahua; 1.1 mi S Colonel Alvaro Obregon; Ciudad Delicias; 3 mi SE*

Ciudad Delicias; 10 mi S Ciudad Delicias; El Herradero; Gallego; 8 mi S Gallego; 10 mi W Gallego; Garcia; Hidalgo del Parral; 8 mi NE Hidalgo del Parral; 25 mi W Hidalgo del Parral; 44 mi S Hidalgo del Parral; Huejotitlan; 6 mi WSW Jiménez; 10 mi N Jiménez; 24 mi N Jiménez; La Bufa; 11.1 km S RR at La Junta; Madera; Marqueño; Matachic; 6 mi NE Meoquí; Moctezuma; Nuevo Casas Grandes; 43 mi SE Nuevo Casas Grandes; 45 mi NW Nuevo Casas Grandes; 2 km W Oginaga, Río Conchos; 7 mi E Pedernales; Salaices; Samalayuca; San José Babicora; Santa Barbara; 63 mi W Santa Barbara; Santa Clara; Santa Clara Canyon, 5 mi W Parrita; Valle de Olivos; Valle de Zaragoza; 23 mi N V. Ahumada; 15 mi S V. Matamoras. *Coahuila*: 10 mi S Allende; 10 mi S Ciudad Acuña; Arroyo de la Zorra; 20 mi SE Arteaga; Boquillas del Carmen; 14.3 mi S Castaños; Guadalupe; 12 mi N Hermanas; La Gloria, S of Monclova; Nueva Rosita; Saltillo; 1 mi E Saltillo; 1 mi SE Saltillo; 4 mi S Saltillo; 6 mi NE Saltillo; 7 mi SSW Saltillo; 12.4 mi S Saltillo; 15 mi N Saltillo; 15 mi S Saltillo; 16 mi SE Saltillo; 17 mi SE Saltillo; 20 mi SE Saltillo; 29 mi SE Saltillo; 39 mi W Saltillo; 66 km S Saltillo; 5 km N San Esteban; San Jose de la Niña; San Pedro de las Colonias; 12 mi SE San Pedro de las Colonias; Serranas del Burro; Torreón; 22 mi N Zaragoza. *Durango*: 8 mi S Canutillo; 30 mi N Cuencamé; 14 mi S Donata Guerra; Durango; 11 mi W Durango; 20 mi W Durango; 25 mi S Durango; 69 mi N Durango; Encino; Guadalupe Victoria; La Loma; 2 mi S Menores de Arriba; Navajos, 20 mi E El Salto; Nombre de Dios; 18 mi SE Nombre de Dios; Pedricena; 3 mi NW Pedricena; Rodeo; San Juan del Río; Santa Lucia; 5 mi NE Sauz. *Guanajuato*: León. *Guerrero*: Iguala. *Hidalgo*: Tasquillo. *Jalisco*: 2 mi S Ciudad Guzmán; Lagos de Moreno; 5.6 mi NE Lagos de Moreno; 13 mi SW Lagos de Moreno; San Juan de los Lagos; 1 mi NE V. Hidalgo. *Michoacán*: 10.3 mi W Morelia; Zamora. *Morelos*: Ruinas Xochicalco; Tepoztlán. *Nayarit*: San Blas. *Nuevo León*: Apodaca; Aramberri; 3 mi E Galeana; Hacienda Vista Hermosa, V. Santiago; 9 mi W Iturbide; Linares; 10 mi S Linares; 15 mi W Linares; 16 mi S Linares; 1.7 mi S Montemorelos; 15 mi SE Montemorelos; Monterrey; 4 mi S Monterrey; 5 mi S Monterrey; 6 mi S Monterrey; 10 mi W Monterrey; Paso Mamulique; Peña Nevada Zaragoza; Pesqueria; 10 mi N Providencia; 41 mi S Sabinas Hidalgo; 22 mi S San Roberto; 40 mi S San Roberto; 46 mi NW San Roberto; Santiago; Vallecillo. *Oaxaca*: 3 mi SE El Tule; 10 mi N Miltepec; Mitla; Oaxaca; 2 mi NW Oaxaca; Ruinas Zaachila; 13 km W Tehuantepec; 22 mi SE Totalapán, San José Viejo. *Puebla*: Acatlán; 11 mi SE Acatlán; 19 mi NW Calcalcapan; Chilac; Puebla; 6 mi SW Tehuacán; 7 mi NE Tehuacan; Valseguillo. *Querétaro*: Oro. *San Luis Potosí*: 3 mi W Cedral; 12 mi W Ciudad del Maíz; 20 mi S Ciudad Valles; 19.6 mi N El Huizache; 28.5 mi S El Huizache; El Salto; 34 mi S Salinas; 10 mi NE San Luis Potosí; 31 mi S San Luis Potosí; 46 mi N San Luis Potosí; 84 mi NE San Luis Potosí; 123 mi NE San Luis Potosí; V Hidalgo; 12 mi NE V. Hidalgo. *Sinaloa*: Los Mochis; 5 mi N Mazatlán; 46 mi E Mazatlán. *Sonora*: 20 mi SE Agua Prieta; 65 mi SE Agua Prieta; Alamos; 7 mi SE Alamos; 7 mi W Alamos; 10 mi W Alamos; Bahía Kino; 1 mi W Caborca; Cabullona; Campo Utah; El Desemboque; El Fuerte; 5 mi E Esqueda; 20 mi S Estacion Llano; Guaymas; 26 mi SE Guaymas; Hermosillo; 40 mi N Hermosillo; 42 mi S Hermosillo; 9 mi NNE Imuris; La Chiripa; La Choya; La Floresta Ranch, 8 mi E Tastiota; Magdalena; Minas Nuevas; Mira Mar Beach; Navojoa; 5 mi E Navojoa; Nogales; Palm Canyon, 17 mi E Magdalena; Pitiquito; Pozo Coyote; Puerto Peñasca; San Bernardino, Río Mayo; 8 mi S Santa Ana; Santa Rosa Ranch; Santa Teresa; Sonora; 20 mi S Sonoyta;

38 km S Sonoyta; Tastiota; Tiburón Island; V. de Seris, 5 mi SW Hermosillo; Yavaros. *Tamaulipas*: Ciudad Victoria; 25 mi S Ciudad Victoria; 81 mi NW Ciudad Victoria; 35 km N El Limon; Gómez Fariás; Guemes, 15 mi N Ciudad Victoria; Lago Republica Española; Matamoros; San Fernando; San José. *Veracruz*: 1 mi NE Acultzingo; Orizaba. *Zacatecas*: 4 mi NE Concepción del Oro; Fresnillo; 1 mi N Fresnillo; 8 mi S Fresnillo; 9 mi S Fresnillo; 25 mi W Fresnillo, Laguna Balderama; 14 mi N Luis Moya; Sain Alto; 28 mi NE Sierra Viejo.

**GUATEMALA:** *Jutiapa*: 6 mi NE El Progreso.

**Comments.** This subspecies is extremely variable and has been the subject of much confusion in the past. Its relationship with the nominate subspecies is discussed under the comments section of that subspecies.

Ruckes (1957a) divided *T. pallidovirens* into four subspecies: *pallidovirens* from the far western U.S.; *setosa* from the northwestern U.S.; *spinosa* from the southwestern U.S. and Mexico; and *accerra* from the eastern U.S. Ueshima (1963) showed that specimens of *pallidovirens* from California have a different chromosome number than specimens from the eastern U.S. (14 + XY in the male versus 16 + XY, respectively). Because of this difference, he believed that the two populations were genetically isolated and were probably two distinct species. The difference in chromosome number has been confirmed in the present study. Cross-breeding and free-choice mating experiments also have been conducted, the results of which support the separation of the two taxa into distinct species (e.g., specimens from California and Louisiana mated and laid eggs, but the eggs were infertile).

Ruckes (1957a) described *T. pallidovirens setosa* from Idaho and eastern areas of Oregon and Washington. During this study, specimens from Nez Perce Co., Idaho were karyotyped. They had a chromosome complement of 14 + XY in the male, the same as *T. pallidovirens* from California.

Ruckes (1957a) described *T. pallidovirens spinosa* from the southwestern U.S. Ueshima (1963) karyotyped specimens of this form collected from southeastern California. He found that males had a chromosome complement of 14 + XY, and he concluded that the designation of *spinosa* as a subspecies of *T. pallidovirens* was probably correct. During the present study, however, specimens karyotyped from several localities in southern Arizona were found to have a chromosome complement of 16 + XY. Also, in cross-breeding experiments, specimens from Arizona and Louisiana readily interbred with no apparent difficulties and produced viable young. Therefore, it is probable that *spinosa* is *T. custator accerra*, not *T. pallidovirens*.

Ruckes (1957a) used the spinose humeral angles of *T. pallidovirens spinosa* to separate it from *T. custator accerra* (=his *T. p. accerra*). This character is relatively variable, however. Long series from many localities within the range of *spinosa* usually include specimens with spinose humeral angles and specimens with rounded humeral angles, as well as many intermediates. Geographical separation of the two forms is not complete, and therefore *spinosa* is placed as a junior synonym of *T. c. accerra*.

Distinguishing *T. custator accerra* and *T. pallidovirens* can be difficult. In general, specimens of *T. c. accerra* (excluding the *spinosa* form) have a postspiracular black spot on each side of each abdominal sternite, while specimens of *T. pallidovirens* do not. However, some (<10%) specimens of *T. pallidovirens* have postspiracular black spots, but the spots are usually smaller than the adjacent spiracle. Conversely, some

(<10%) specimens of *T. c. accerra* lack postspiracular black spots. Fortunately, the two species are geographically separated except in the southwestern U.S., where *T. pallidovirens* overlaps considerably with the *spinosa* form of *T. c. accerra*. These two forms can usually be separated by the degree of spinosity of the humeral angles. *Thyanta pallidovirens* always has rounded humeral angles, while the *spinosa* form of *T. c. accerra* usually has angulate to spinose humeral angles. Also, most specimens of *T. pallidovirens* have at least a partial reddish transhumeral band, a condition that is rare in the *spinosa* form of *T. c. accerra*.

*Thyanta (Thyanta) pallidovirens* (Stål)

Figs. 48–62, Map 4

*Pentatoma pallidovirens* Stål, 1859:227; Walker, 1867:288.

*Thyanta pallidovirens*: Stål, 1862a:58; Stål, 1872:35; Uhler, 1886:7; Lethierry and Severin, 1893:148; Uhler, 1894a:231; Van Duzee, 1904:53–54; Banks, 1910:90 (part); Van Duzee, 1917:52; Torre-Bueno, 1939:232; Ruckes, 1957a:1–22, Froeschner, 1988:593.

*Thyanta custator* (of authors, not Fabricius): Uhler, 1872:399 (part); Uhler, 1876: 289–290 (part); Kirkaldy, 1909:94 (part); Van Duzee, 1914:4–5 (part); Van Duzee, 1916:231; Van Duzee, 1917:52 (part).

*Thyanta pallidovirens setosa* Ruckes, 1957a:17–18; Froeschner, 1988:593. NEW SYNONYMY.

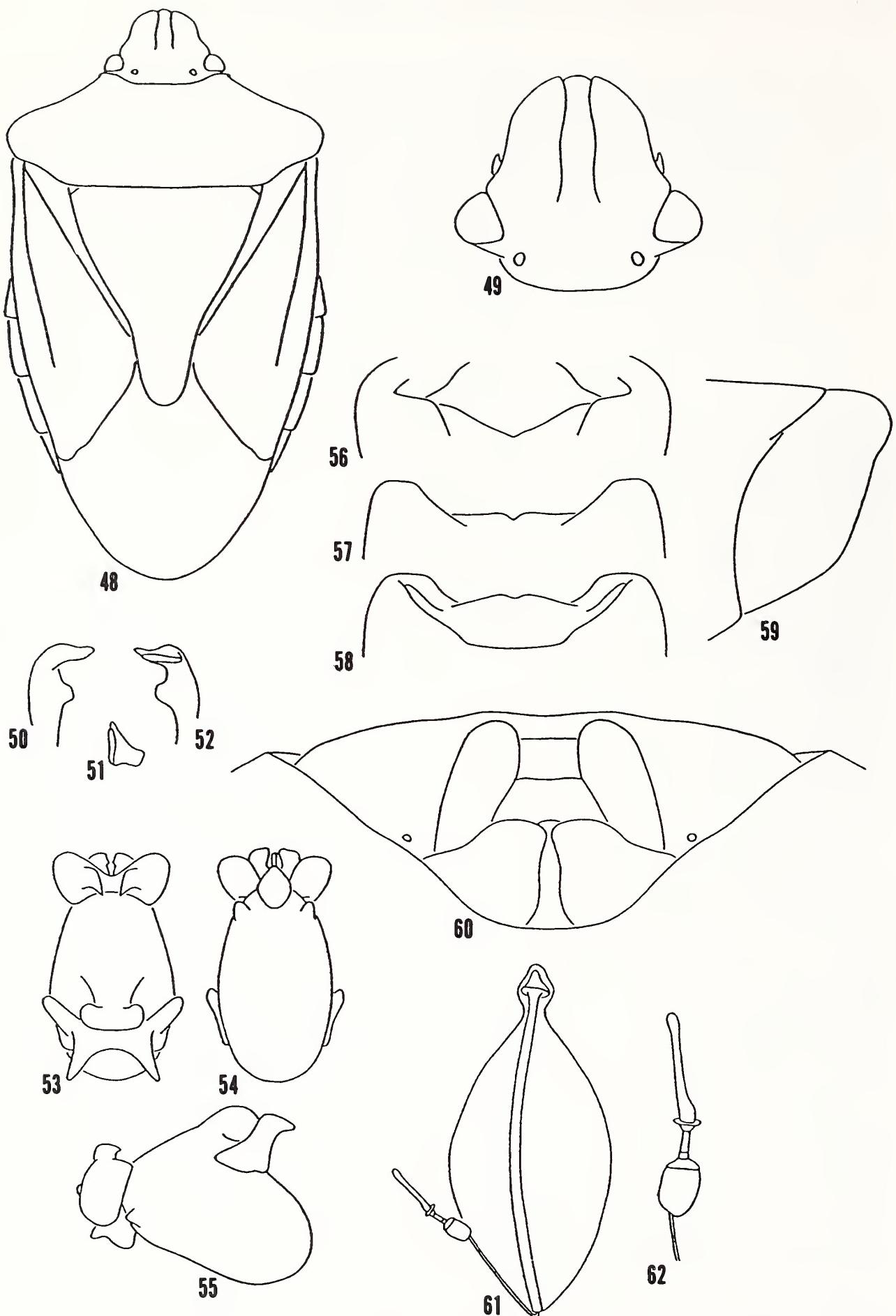
**Diagnosis.** Dorsal coloration often with varying amounts of reddish between humeral angles, often extending onto basal margin of each corium and along anterolateral pronotal margins; sometimes apex of scutellum reddish.

Lateral jugal margins sinuous, not parallel (Fig. 49). Anterolateral margins of pronotum straight to slightly concave in dorsal view, green to reddish, never piceous; humeral angles rounded (Fig. 48); pronotal cicatrices immaculate. Postspiracular black spots usually lacking; if present, then usually smaller than adjacent spiracle. Posterolateral angles of abdominal sternites immaculate.

Basal plates in caudoventral view with mesial margins straight to slightly concave; posterior margins sinuous; posteromesial angles narrowly rounded (Fig. 60). Posterolateral angles of pygophore continuing onto posteroventral surface of pygophore as carinae, forming rectangular impression; posterior margin slightly concave in caudal view, usually with small, medial, V-shaped emargination (Fig. 56); posterolateral angles prominent in ventral and dorsal views (Figs. 57, 58); pygophore slightly concave in lateral view (Fig. 59).

**Types.** Stål (1859) described *Pentatoma pallidovirens* from 1♂ and 1♀ specimen from California without designating a holotype or paratype. The ♂ specimen labeled (a) "California" (b) "Kinb." (c) "Type" (d) "Typus" (e) "Thyanta pallidovirens Stål" (f) "109 51" (g) "349 84" (h) "Riksmuseum Stockholm" is designated the lectotype. The ♀ specimen labeled (a) "California" (b) "Kinb." (c) "♀" (d) "Type." (e) "Allo-typus" (f) "350 84" (g) "Riksmuseum Stockholm" is designated paralectotype. The lectotype and the paralectotype, which are conserved in the Naturhistoriska Riks-museet (Stockholm, Sweden), were examined.

Ruckes (1957a) described *T. pallidovirens setosa* from 18♂♂ and 10♀♀ specimens.



Figs. 48–62. *T. pallidovirens*. 48. Habitus. 49. Head. 50–52. Right paramere. 50. Medial view. 51. Ectal view. 52. Lateral view. 53–55. Theca and related structures. 53. Ventral view. 54. Dorsal view. 55. Lateral view. 56–59. Pygophore. 56. Caudal view. 57. Ventral view. 58. Dorsal view. 59. Lateral view. 60. Genital plates, caudoventral view. 61. Spermatheca. 62. Spermathecal pump.



### Map 4

Map 4. *T. pallidovirens*.

The holotype, which was examined, is from Pullman, Whitman Co., Washington, and is deposited in the American Museum of Natural History (New York).

*Distribution.* Western U.S. (Map 4).

*Specimens examined.* 3,606 specimens collected during every month of the year; deposited in AMNH, CAS, DAR, EGER, FMNH, FSCA, INHS, ISU, LACM, LHR, LSU, MSU, MSUB, MSUE, NCSU, ODAS, OSUC, PUL, SIUC, SMEK, TAMU, UCB, UCR, UCS, UGA, UIM, UNAM, USNM, UUSL, WSU. CANADA: British

*Columbia*: Cache Ck; Coldstream; Comox; Lytton; Malahat; Nanaimo; Vancouver Isl; Royal Oak; Saanich Dist; Vernon; Victoria; Wellington.

UNITED STATES: California: *Alameda, Alpine, Amador, Butte, Calaveras, Colusa, Contra Costa, El Dorado, Fresno, Glenn, Humboldt, Inyo, Kern, Lake, Lassen, Los Angeles, Madera, Marin, Mariposa, Mendocino, Merced, Modoc, Mono, Monterey, Napa, Nevada, Orange, Placer, Plumas, Riverside, Sacramento, San Benito, San Bernardino, San Diego, San Francisco, San Joaquin, San Luis Obispo, San Mateo, Santa Barbara, Santa Clara, Santa Cruz, Shasta, Sierra, Siskiyou, Solano, Sonoma, Stanislaus, Tehama, Trinity, Tulare, Tuolumne, Ventura, Yolo, Yuba*. Idaho: *Ada, Benewah, Bingham, Blaine, Boise, Bonner, Butte, Cassia, Clearwater, Elmore, Franklin, Fremont, Gem, Gooding, Idaho, Kootenai, Lake, Latah, Lewis, Nez Perce, Oneida, Owyhee, Shoshone, Twin Falls, Valley*. Montana: *Lake, Lewis & Clark, Ravalli, Sanders*. Nevada: *Carson City, Douglas, Lyon, Washoe*. Oregon: *Baker, Benton, Crook, Curry, Deschutes, Douglas, Grant, Harney, Hood River, Jackson, Jefferson, Josephine, Klamath, Lake, Linn, Malheur, Marion, Multnomah, Polk, Sherman, Tillamook, Umatilla, Union, Wasco, Washington, Wheeler, Yamhill*. Utah: *Box Elder, Cache, Garfield, Morgan, Salt Lake, Sevier, Utah, Washington, Wheeler, Yamhill*. Utah: *Box Elder, Cache, Garfield, Morgan, Salt Lake, Sevier, Utah, Washington, Weber*. Washington: *Asotin, Benton, Chelan, Clark, Columbia, Douglas, Grant, King, Kittitas, Mason, Okanagon, Pierce, San Juan, Snohomish, Spokane, Thurston, Walla Walla, Whitman, Yakima*.

**Comments.** Ruckes (1957a) distinguished *T. pallidovirens setosa* from other U.S. *Thyanta* by the increased amount of pilosity on the legs and rostrum. This is a difficult character to discern. The brown autumnal-vernial forms of several other species and subspecies are also characterized by more and longer hairs on the same body structures (McPherson, 1979a). Because *T. p. setosa* differs from the nominate subspecies in no other significant manner, *T. p. setosa* is placed as a junior synonym of *T. pallidovirens*.

No reliable morphological character will consistently separate *T. pallidovirens* from *T. custator accerra*, as discussed in detail under the comments section of *T. c. accerra*. Basically, in the southwestern U.S. the two usually can be separated by the shape of the humeral angles, which are rounded in *T. pallidovirens* and angulate to spinose in *T. c. accerra*. In the northwestern U.S., the two species seem to be geographically isolated (Maps 3, 4). Here, separation often can be made based on the presence (in *T. c. accerra*) or absence (in *T. pallidovirens*) of postspiracular black spots.

*Thyanta (Thyanta) perditor* (Fabricius)  
Figs. 63–77, Map 5

*Cimex perditor* Fabricius, 1794:102; Fabricius, 1803:163.

*Pentatoma fascifera* Palisot de Beauvois, 1817:150, fig. 8 (syn. by Dallas, 1851:206).

*Pentatoma collaris* Westwood, 1837:40 (syn. by Dallas, 1851:206).

*Cimex transversalis* Herrich-Schäffer, 1841:66 (syn. by Dallas, 1851:206).

*Cimex dimidiatus* Herrich-Schäffer, 1841:fig. 629 (syn. by Dallas, 1851:206).

*Pentatoma dimidiatum*: Herrich-Schäffer, 1844:94 (syn. by Dallas, 1851:206).

*Euschistus perditor*: Dallas, 1851:206; Walker, 1867:247.

*Pentatoma (Mormidea) perditor*: Guérin-Méneville, 1857:367.

*Thyanta perditor*: Stål, 1862a:58; Stål, 1862b:104; Stål, 1868:29; Stål, 1872:34; Uhler, 1872:399 (part); Uhler, 1876:289; Uhler, 1877:404 (part); Distant, 1880:66; Berg, 1884:100; Distant, 1893:333; Lethierry and Severin, 1893:148; Uhler, 1893:705; Uhler, 1894a:230 (part); Uhler, 1894b:173; Distant, 1900:432; Van Duzee, 1904: 52–53 (part); Van Duzee, 1907:9; Kirkaldy, 1909:95; Banks, 1910:90; Zimmer, 1912:14 (part); Barber, 1914:523; Van Duzee, 1917:51–52; Barber, 1923:12; Blatchley, 1926:113, 114–115 (part); Barber, 1939:292–293; Torre-Bueno, 1939: 230; Ruckes, 1957a:1, 20; Froeschner, 1988:593.

*Euschistus fasciatus* Walker, 1867:245 (syn. by Stål, 1872:34).

*Euschistus adjunctor* Walker, 1867:249 (syn. by Stål, 1872:34).

*Thyanta (Thyanta) perditor*: Rider and Chapin, 1991.

**Diagnosis.** Transhumeral rubiginous band usually present; tylus and vertex of head often reddish.

Lateral jugal margins sinuous, not parallel (Fig. 64). Humeral angles spinose, each spine directed anterolaterad; anterolateral pronotal margins not piceous, concave in dorsal view (Fig. 63). Mesial corner of each pronotal cicatrice black. Each abdominal sternite with postspiracular black spot on each side, both anterolateral and postero-lateral angles usually piceous.

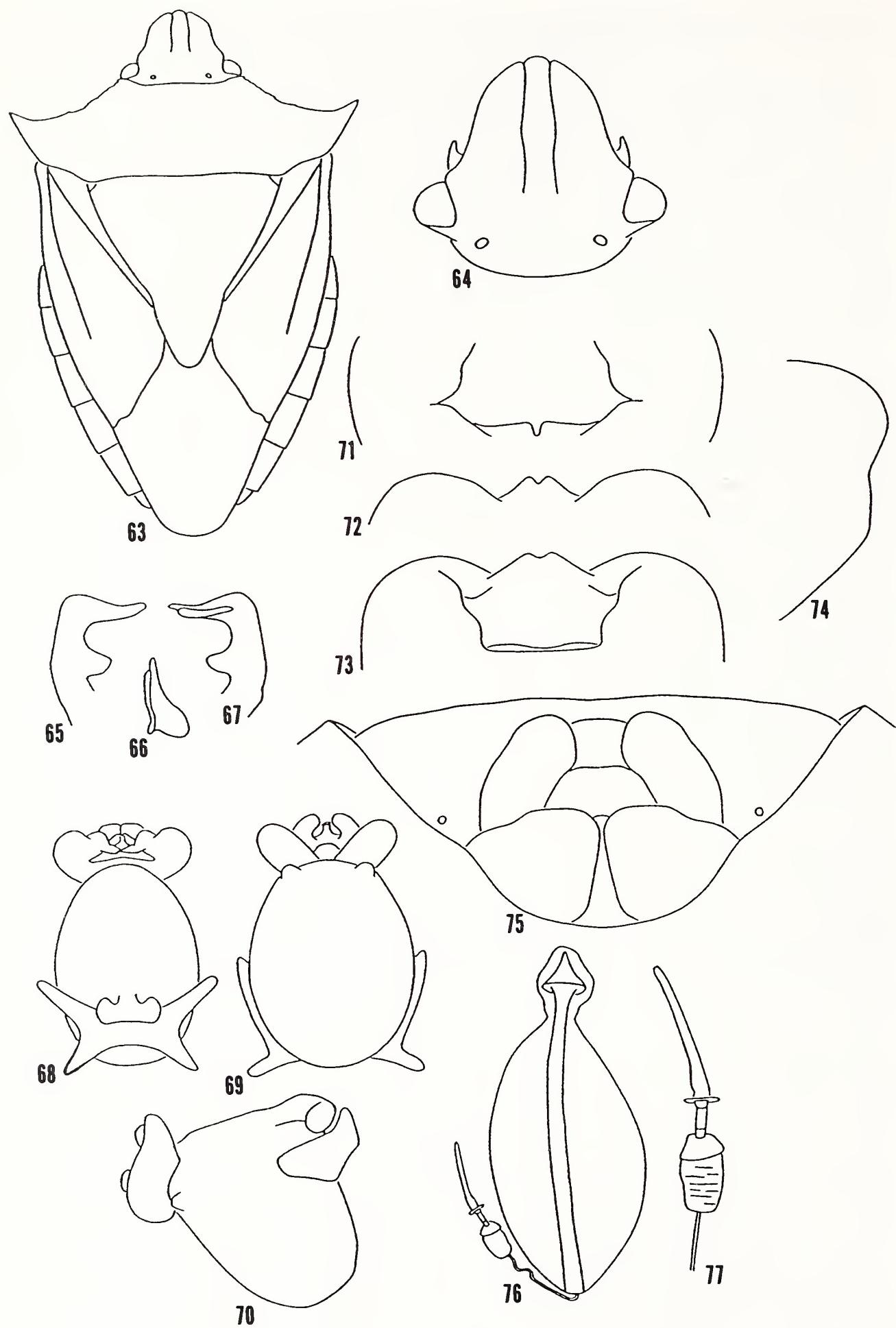
Basal plates with mesial margins straight to slightly convex in caudoventral view; posterior margins sinuous (Fig. 75). Pygophoral opening subtended by semicircular impression; posterior margin of pygophore produced posterodorsad, in ventral and dorsal views convex medially with small, medial, V-shaped emargination (Figs. 72, 73), concave in lateral view (Fig. 74).

**Types.** Fabricius (1794) described *Cimex perditor* from 2♂♂ and 2♀♀ specimens without designating a holotype or paratypes. Rider and Chapin (1991) made lectotype and paralectotype designations. All four specimens, which are housed in the Universitetes Zoologiske Museum (Copenhagen, Denmark), were examined.

Rider and Chapin (1991) confirmed the status of *Pentatoma fascifera* Palisot de Beauvois, *P. collaris* Westwood, *Cimex transversalis* Herrich-Schäffer, *Euschistus fasciatus* Walker, and *E. adjunctor* Walker as junior synonyms. They also designated lectotypes for the latter two species. At one time *Euschistus rubiginosus* Dallas was considered a synonym of *T. perditor*. Rider (1986b), however, examined the holotype of *E. rubiginosus* and determined that it was a senior synonym of *Euschistus incus* Rolston.

**Distribution.** This is the most widely distributed species in the genus, occurring from southern Florida, Texas, and Arizona south through Central America, West Indies, and South America to northern Argentina (Map 5).

**Specimens examined.** 844 specimens collected during every month of the year; deposited in AMNH, AUA, BMNH, CAS, CNC, CU, DAR, DBT, FSCA, INHS, ISU, LHR, LSU, MSU, MSUE, OSUC, PUL, SIUC, SMEK, TAMU, UAT, UCB, UCR, UCS, UGA, UMAA, UMC, UNAM, USNM, WSU. UNITED STATES: Arizona: Cochise: Southwest Research Station, 5 mi W Portal. Florida: Flamingo; Mahogany Hammock; Paradise Key; Pine Castle; Windly. Broward: Deerfield Beach. Collier: Immokalee; Royal Palm Park. Dade: Coral Gables; Everglades National Park; Florida City; 5 mi SW Florida City; Goulds; Grossman Hammock; Hialeah; Homestead; Kendall; Miami; Miami Springs; Princeton. Highlands: Avon Park; Lake Plac-

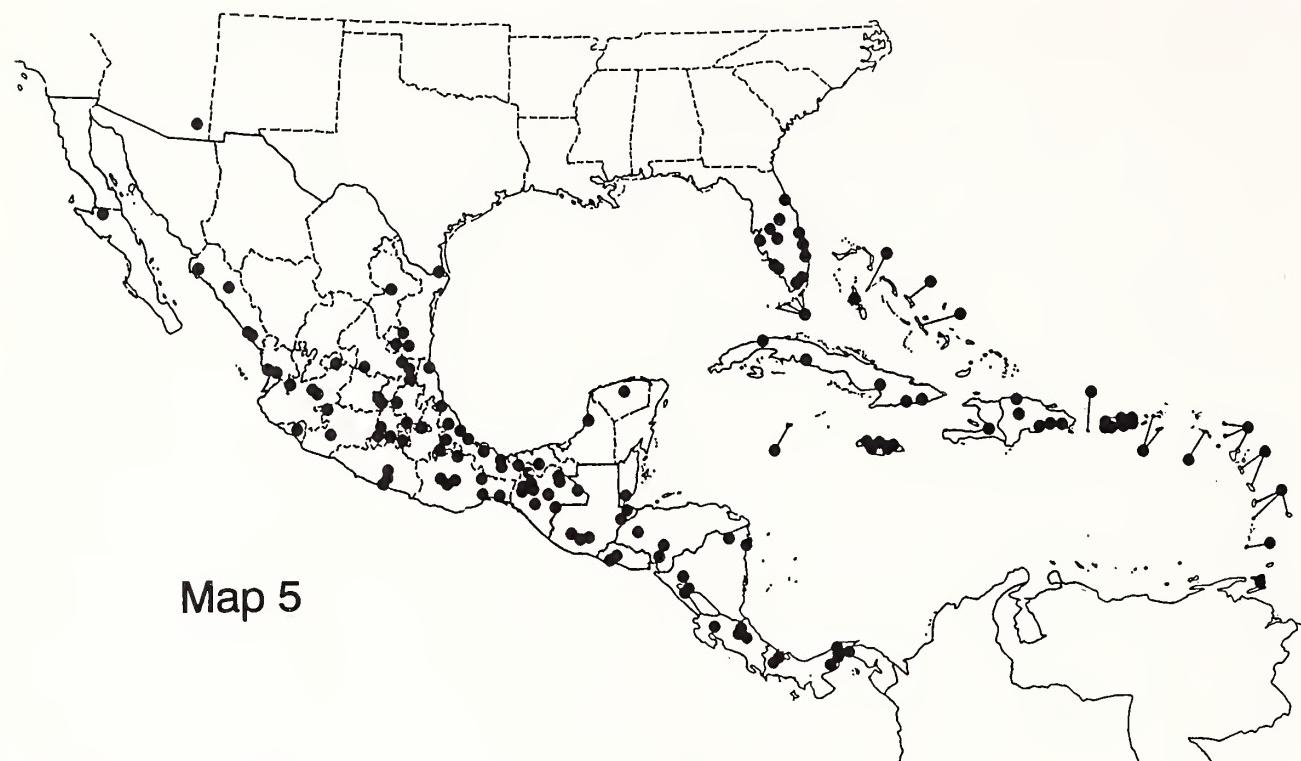


id; Sebring. *Indian River*: Vero Beach. *Lee*: Fort Myers. *Manatee*: Palmetto; Terra Ceia. *Martin*: Stuart. *Monroe*: Big Pine Key; Key Largo; Key West; Marathon Key; Upper Key Largo; Upper Matecumbe Key. *Orange*: Orlando. *Palm Beach*: Belle Glade; Delray; Royal Palm Park. *Polk*: Lake Hamilton; Lakeland. *Volusia*: Daytona Beach. *Texas*: *Cameron*: Brownsville; Sabal Palm Grove near Southmost.

**MÉXICO:** Hochmilco; Lagos de Moreno; Paricutin. *Aguascalientes*: Aguascalientes. *Campeche*: km 71 Carr. Campeche-Meizina. *Chiapas*: Arriaga; 4.4 mi N Bochil; Bonampak Ruinas; Chicoasen; Chorreadera State Park; Cintalpa; 5 mi S Cintalpa; 13 mi W Cintalpa; Comitán; 31.5 mi SE Comitán; Dos Lagos; El Sumidero; 1.6 mi S Jitotol; 13 mi S La Trinitario; 18 km S La Trinitario; 12 mi W Ocozocoautla; Palenque; Palenque Ruinas; 23 mi S Palenque, 4 mi NE Pichucalco; 1 mi S Rayón; 2 mi SE Revolucion Mexicana; 3 mi W Rizo de Oro; Sanches Ranch Las Rosas; San Cristóbal de las Casas; 8 mi SE San Cristóbal las Casas; 23 mi W San Cristóbal de las Casas; 39 mi E San Cristóbal las Casas; Simojovel; 10 km WNW Soyalo; 2 mi E Suchiapa; Sumidero Canyon; 9 mi SE Tapilula; Teopisca; 14 mi N Tuxtla Gutiérrez; 3.5 km S Río Tulija. *Colima*: Colima Volcano. *Durango*: 9 mi W La Ciudad; Peasa Pena. *Guanajuato*: León. *Guerrero*: Acahuizotla; Acapulco de Juárez; 5 mi S, 2.5 mi E Chilpancingo; km 8 Carr. Chilpancingo Omilteme; 17 mi N Mexcala; Mochitlán; 1.5 mi W Mochitlán; 13 mi SW Tierra Colorado. *Hidalgo*: Hwy 45, 17 mi NE Huichapan. *Jalisco*: 16 km E Agua el Obispo; Ajijic; Guadalajara; 5 mi SE Plan de Barrancas. *México*: 4.3 mi NE Ixtapán de la Sal; Tejupilco; Temascaltepec, Real de Arriba; Teotihuacán; 11 mi W Texcoco; 1 mi NE Tlamacas, P. N. Popocatepetl; Valle de Bravo; 21 mi NW Valle de Bravo. *Michoacán*: Apatzingán; 11 mi E Apatzingán; Jiquilpán; Palo Alto; Tancitaro. *Morelos*: Cuautla; Cuernavaca; Jojutla; Morelos; Pte de Itla; Xochicallo. *Nayarit*: 13 mi NW Ahuacatlán; Jesus Maria; Nayarit-Jalisco line, Hwy 15; 15 km E San Blas; Tepic. *Nuevo León*: 9 mi S Monterrey; 3 mi S Pacheco. *Oaxaca*: 7.7 mi S Ejutla; El Camaron, 20 mi E Oaxaca; 2.7 mi NW El Camaron; 10 mi S El Camaron; 27 mi E Juchitán; 3 km E La Ventosa; 3.4 mi SE Matatlán; 11 mi N Matías Romero; SE Nejapa; 30 mi NW Oaxaca; 45 mi SE Oaxaca; 53 mi NE Oaxaca; Tehuantepec; Temazcal; 23 mi W Tequistlán; Totolapán; 18 mi NW Totolapán; 23 km NW Totolapán; Tuxtepec. *Puebla*: 5.1 mi SW Tehuacán; 6 mi SW Tehuacán. *Querétaro*: Querétaro; 29 mi N Querétaro; 10 mi E San Juan del Río. *San Luis Potosí*: 5 mi E Ciudad del Maíz; 11 km N Ciudad Valles; 20 mi S Ciudad Valles; El Pujal; El Salto Falls; Micos; 31 mi S San Luis Potosí; Tamazunchale; 30 mi S Tamazunchale; Valle Hidalgo; 2 mi E Xilita. *Sinaloa*: 22.6 mi S Culiacán; Los Mochis; Mazatlán; 15 mi N Mazatlán; Valle Unión; 5 mi E Valle Unión. *Tabasco*: 30 mi W Cárdenas; Chontalpa; Pajelagatero; Pico do Oro; 5 km S Villahermosa; 14 mi SE Villahermosa. *Tamaulipas*: Bocatoma: 11 mi SW Ciudad Victoria; 6 mi W Río Sabinas, near Encino; 19 mi NE Tula. *Tlaxcala*: 2 mi W Tlaxcala. *Veracruz*: Alvarado; Catemaco; 7 mi SE Catemaco; Coatzacoalcos; Córdoba; 1 mi E Córdoba;



Figs. 63–77. *T. perditor*. 63. Habitus. 64. Head. 65–67. Right paramere. 65. Medial view. 66. Ectal view. 67. Lateral view. 68–70. Theca and related structures. 68. Ventral view. 69. Dorsal view. 70. Lateral view. 71–74. Pygophore. 71. Caudal view. 72. Ventral view. 73. Dorsal view. 74. Lateral view. 75. Genital plates, caudoventral view. 76. Spermatheca. 77. Spermathecal pump.



Map 5

Map 5. *T. perdior*.

Cotaxtla; Extación Mieron das Fortín; 1 mi W Fortín de las Flores; Jalapa; 10 mi E Jalapa; Lake Catemaco; 5 mi N Lerdo de Tejada; Los Tuxtlas Biological Station; L. Rivera. Atzagan; 4 mi NE Minatitlán; Nanchital; Orizaba; Papantla; Plan del Río; 3 mi SW Sontecompaپán; 15.8 mi S Tampico; Vega de Alatorre; Veracruz. Yucatán: 10 km N Pisté.

GUATEMALA: Chocola. Chimaltenango: Yepocapa. Guatemala: Guatemala City. Izabal: Livingston; Los Amates; Morales. Jutiapa: San Jerónimo. Sac.: Antigua Guatemala. Sololá: Panajachel, Lago de Atitlán. Suchitepequez: Alta Vista; 8 mi N Santa Bárbara. BELIZE: Punta Gorda. EL SALVADOR: La Libertad; San Salvador. HONDURAS: 1 mi W Jicaro Galan Junction, Rio Nacaome; Tegucigalpa; Uyace Peak; Yojoa Lake; Zomorano. NICARAGUA: km 4 to Masaya. Estelí: 13.4 mi NW Sebaco. León: Los Zarzales; Malpaisillo. Managua: Los Brasiles; Managua; Tipitapa. Musawas: Waspuk R. Zelaya: Puerto Cabezas. COSTA RICA: Isla Bonita; Reventazon Valley; San Carlos. Cartago: Santiago; Turrialba. Guanacaste: La Pacifica near Cañas. Heredia: Heredia; 2 mi E Puerto Viejo; Varablanca. Puntarenas: Monteverde. San José: 5.5 km SE Desamparados; San José. PANAMA: New California. Bocas del Toro: Chiriquí Grande. Canal Zone: Barro Colorado Island; Cristóbal. Chiriquí: Boquete; Cerro Punta; Porteillos. Coclé: Cerro Pena near El Valle. Panamá: Cerro Jefe; Madden Lake.

BAHAMA ISLANDS: Andros Island: Andros Town. Cat Island. Long Island: Clarencetown. New Providence Island: Nassau. CUBA: El Cobre. Ciudad de la Habana: La Habana. Cienfuegos: Palmira; Soledad nr Cienfuegos. Granma: Cayamas. Guantánamo: Mtns nr Guantánamo. Las Tunas: Jobabo. Pinar del Río: San Vicente. Santiago de Cuba: 12 mi N Santiago de Cuba. JAMAICA: Balaclava; Claremont Baron Hill Trelawny; Hope Bay; Kingston; Liguanea Plain; Mandeville; Montego

Bay. HAITI: *Ouest*: Kenscoff; Port-au-Prince. DOMINICAN REPUBLIC: 8 mi up Macorís River. *Distrito Nacional*: Santo Domingo. *La Romana*: La Romana Center. *La Vega*: Jarabacoa. *Peravia*: 2 km N Nizao; 21 km NW San José. *Puerto Plata*. *San Cristóbal*: San Cristóbal. *San Pedro de Macorís*: Boca Chica. PUERTO RICO: Cialitos Cruces, El Verde, Mona Island. *Aguadilla*: Añasco, Isabela, Rincón, San Sebastián. *Arecibo*: 7 km S Ciales, Dorado, Manatí, Utuado, Vega Baja. *Bayamon*: Corozal. *Guayama*: Arroyo. *Humacao*: Humacao, Loíza, 1 mi SE Luquillo, Naguabo. *Mayagüez*: Boqueron, Guánica Forest, Guayanilla, Mayagüez, San Germán. *Ponce*: Coamo Springs, Juana Díaz, Ponce, 3 mi N Santa Isabel. *San Juan*: Río Piedras. U.S. VIRGIN ISLANDS: *St. Croix*: Frederiksted. *St. Thomas*. BRITISH WEST INDIES: *Antigua*: Bello. *Barbuda*: Codrington. *Dominica*: Castle Bruce Road nr Savane David; Clarke Hall Est; 4.7 mi E Pt Casse; 5 km SW Pt Casse; Roseau. *Grand Cayman*: 3 mi N Georgetown; Western Dist. *Grenada*: Grand Anse; Mount Gay Est; St. Georges. *St. Kitts*: Basseterre; 4 mi W Basseterre. *St. Lucia*: Castries. *St. Vincent*. *Trinidad*: Cumuto; St. Augustine. FRENCH WEST INDIES: *Guadeloupe*: Pointe-à-Pitre. *Martinique*: 2 km N St. Pierre. BARBADOS.

*Comments.* *Thyanta perditor* is one of a group of very closely related species, all of which have distinctly spinose humeral angles. The characters used to separate these species are sometimes subtle and hard to diagnose unless a series of specimens is available. Fortunately, most have very little overlap in their distributional ranges.

*Thyanta (Thyanta) spectabilis* Ruckes  
Figs. 78–92, Map 6

*Thyanta spectabilis* Ruckes, 1957c:175–178, figs. 3–4.

*Thyanta perditor* (of authors, not Fabricius): Van Duzee, 1923:127.

*Diagnosis.* Rubiginous transhumeral band usually present; often tylus and vertex of head reddish.

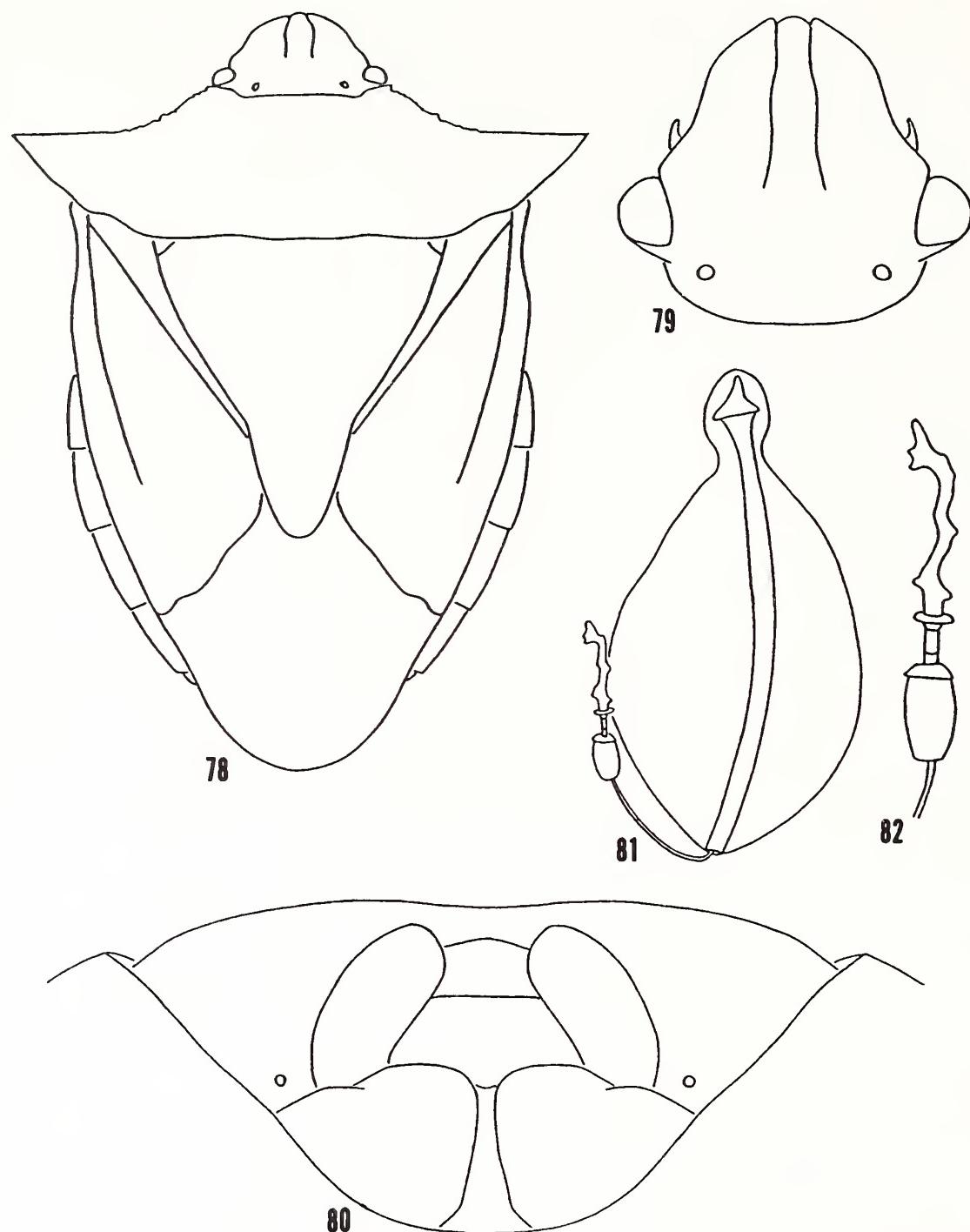
Lateral jugal margins sinuous, not parallel (Fig. 79). Anterolateral pronotal margins concave, not piceous; humeral angles spinose, spines directed primarily laterad and only slightly cephalad (Fig. 78). Mesial corner of each pronotal cicatrice usually piceous. Each abdominal sternite with postspiracular black spot on each side, anterolateral and posterolateral angles piceous.

Basal plates in caudoventral view with mesial margins straight to slightly convex; separated basally; posterior margins sinuous (Fig. 80). Spermathecal bulb digitiform, but with numerous short protuberances (Fig. 82). Pygophoral opening subtended by semicircular impression; posterior margin of pygophore produced posterodorsad, in ventral and dorsal views convex medially with small, medial V-shaped emargination (Figs. 84, 85); slightly concave in lateral view (Fig. 86).

*Types.* Ruckes (1957c) described *Thyanta spectabilis* from 2♂♂ and 6♀♀ specimens, all from Baja California, Mexico. The ♂ holotype was examined and is presently conserved in the California Academy of Sciences (San Francisco).

*Distribution.* Baja California, Mexico (Map 6).

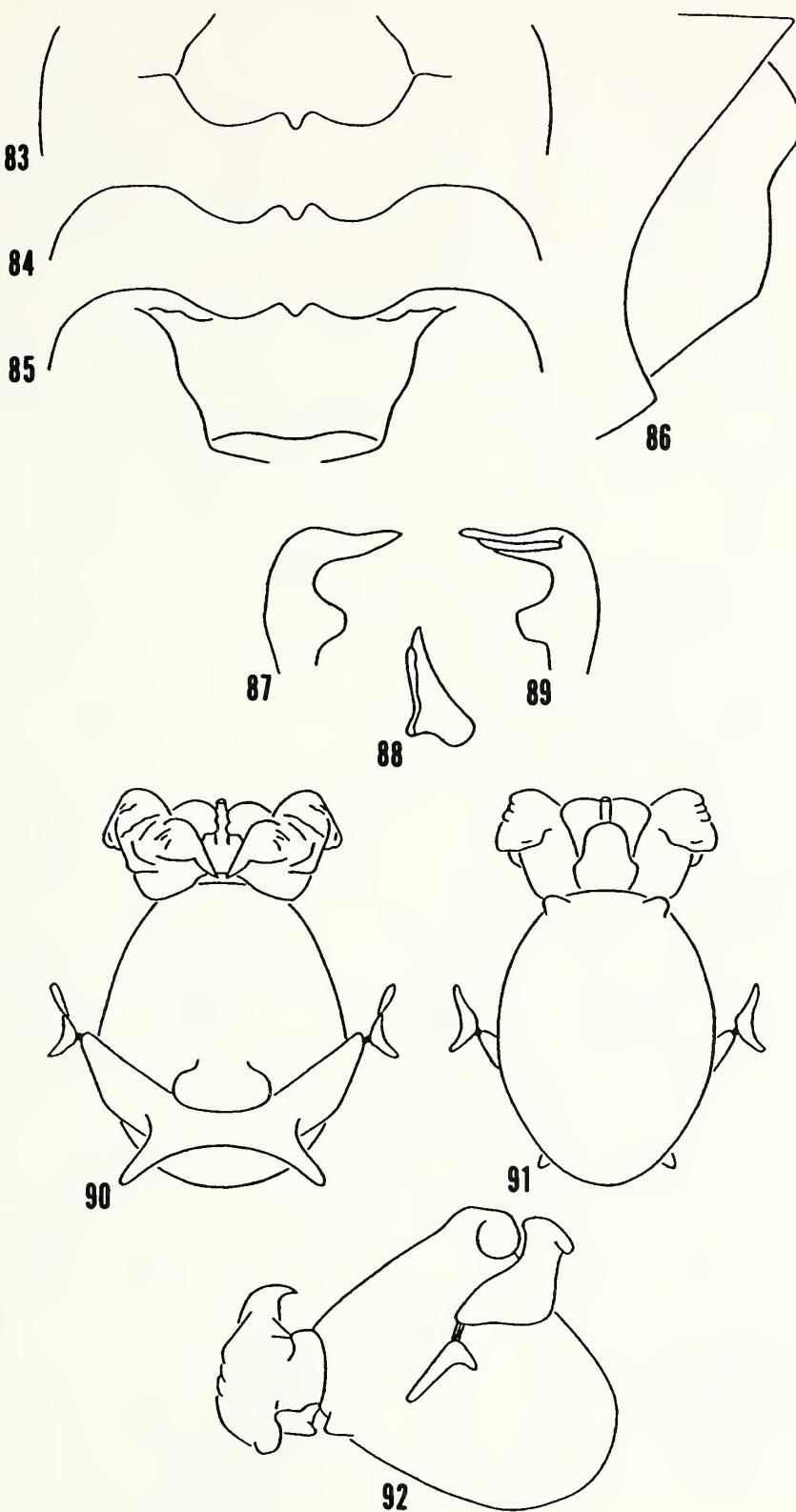
*Specimens examined.* 17 specimens collected during every month of the year except February, April, September, and October; deposited in CAS, DBT, UCB, UIM,



Figs. 78–82. *T. spectabilis*. 78. Habitus. 79. Head. 80. Genital plates, caudoventral view. 81. Spermatheca. 82. Spermathecal pump.

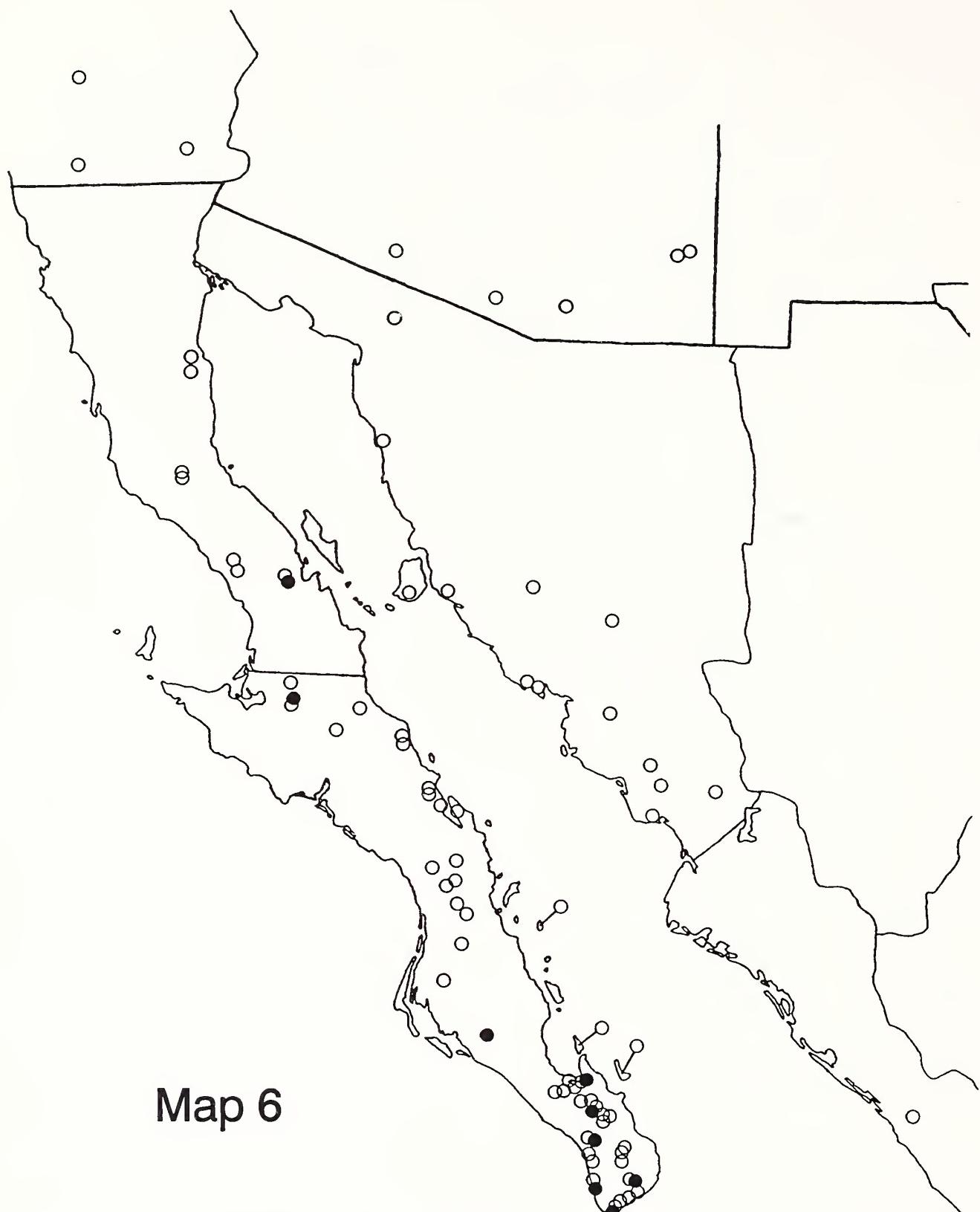
UNAM, USNM. MÉXICO: Lower California; 2 km W El Centenario. *Baja California Norte*: Bahía de los Angeles. *Baja California Sur*: Cabo San Lucas; 28 mi S El Arco Mine, Rancho Santa Marguerita; 2 mi E El Coyote, NE of La Paz; 6 mi S, 1 mi E El Pescadero; La Paz; 6 km S San Pedro; Santa Anita; 7 mi N Santa Anita; 2 km SE, 3.5 km NE Santa Rita; 21.6 mi N Todos Santos; Venancio.

*Comments.* *Thyanta spectabilis* is very closely related to *T. perditor*, and may actually be a subspecies of that species. The genitalia of the two species are virtually identical; the only difference is that the parameres in *T. spectabilis* are somewhat larger than those in *T. perditor*. This is expected, however, since specimens of *T.*



Figs. 83-92. *T. spectabilis*. 83-86. Pygophore. 83. Caudal view. 84. Ventral view. 85. Dorsal view. 86. Lateral view. 87-89. Right paramere. 87. Medial view. 88. Ectal view. 89. Lateral view. 90-92. Theca and related structures. 90. Ventral view. 91. Dorsal view. 92. Lateral view.

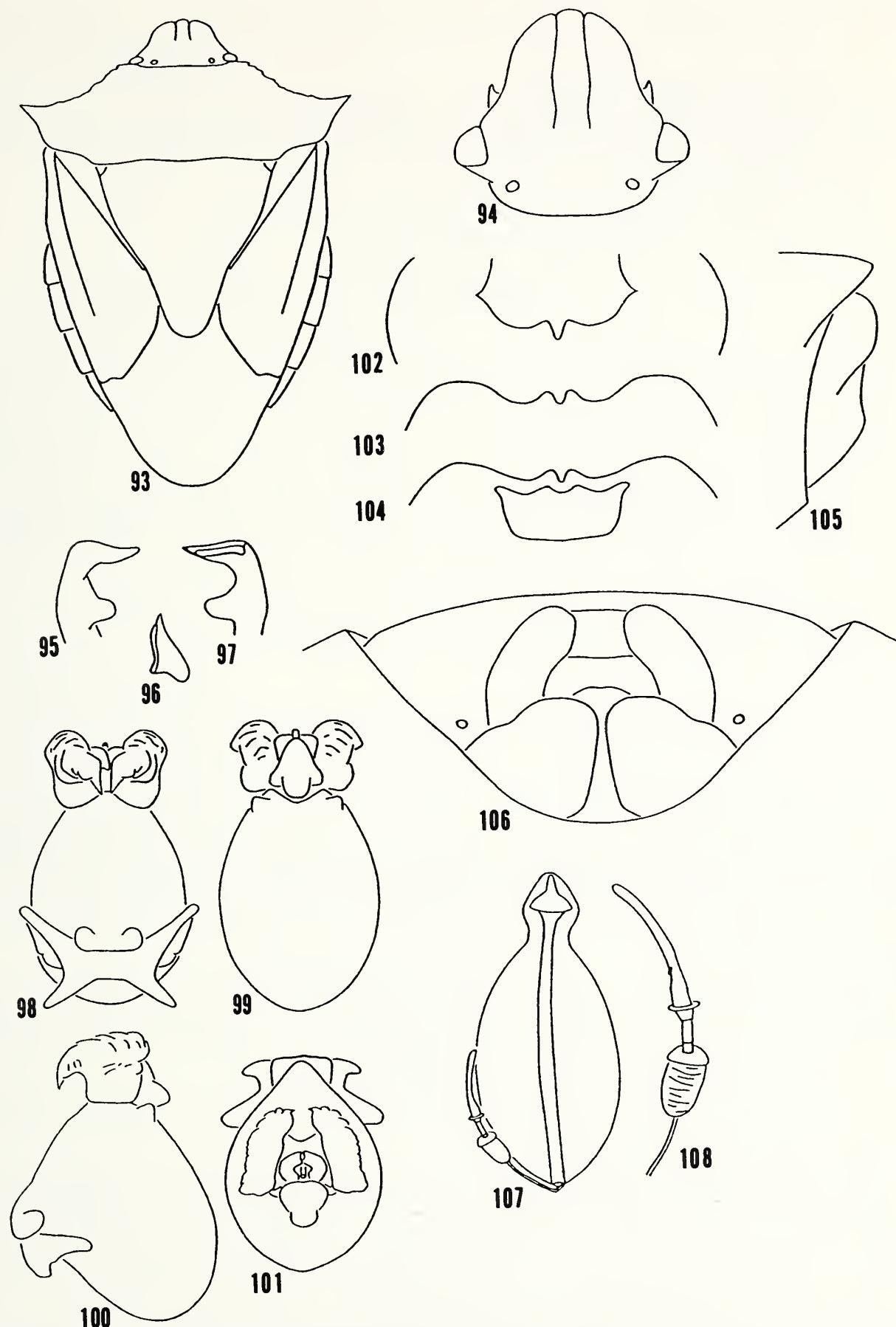
*spectabilis* are larger than those of *T. perditior*. The only reliable character to separate the two species is the orientation of the humeral spine. In *T. perditior* the humeral angle is directed anterolaterad, while in *T. spectabilis* it is directed primarily laterad and only slightly cephalad.



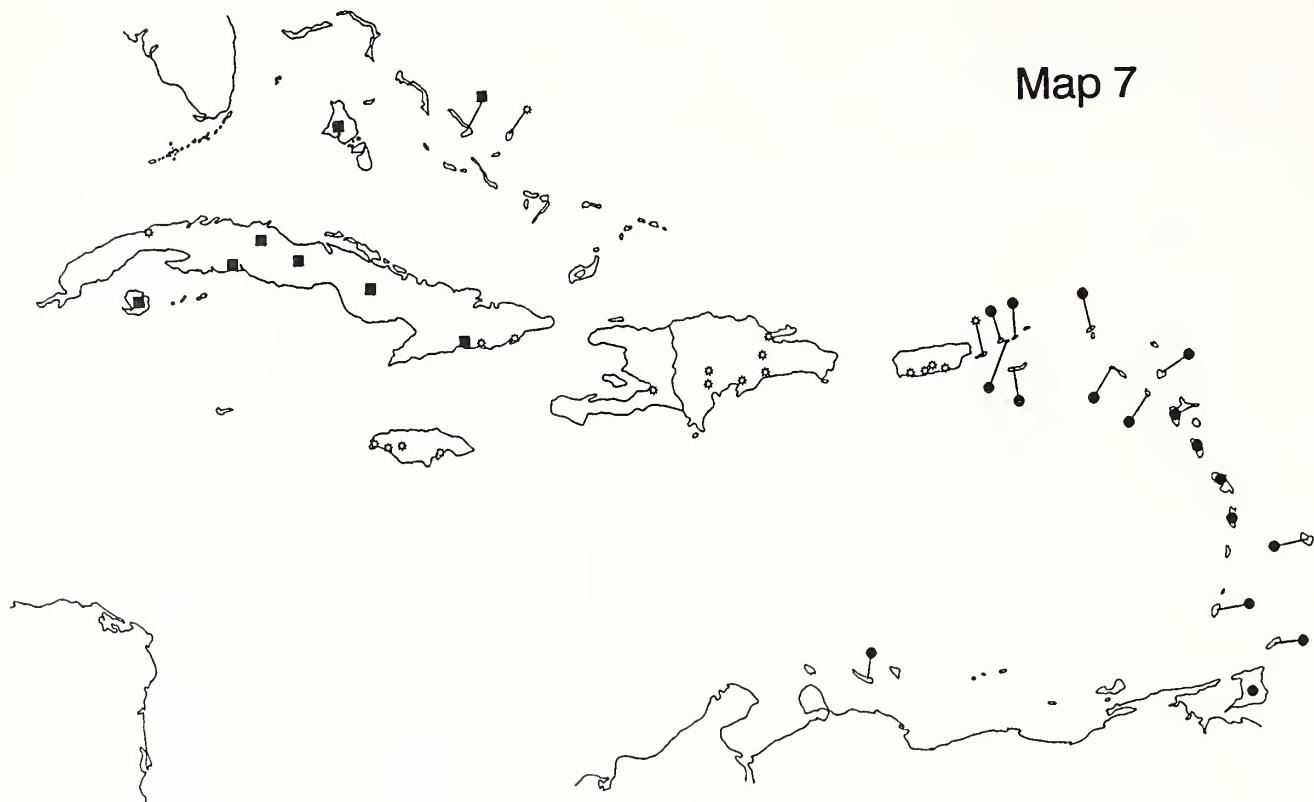
Map 6. *T. planifrons* (○); *T. spectabilis* (●).

*Thyanta (Thyanta) cubensis* Barber & Bruner  
Figs. 93–108, Map 7

*Thyanta cubensis* Barber and Bruner, 1932:257–258, figs. 4–5; Bruner and Barber, 1949:158; Alayo, 1967:18, 20.



Figs. 93–108. *T. cubensis*. 93. Habitus. 94. Head. 95–97. Right paramere. 95. Medial view. 96. Ectal view. 97. Lateral view. 98–101. Theca and related structures. 98. Ventral view. 99. Dorsal view. 100. Lateral view. 101. Ectal view. 102–105. Pygophore. 102. Caudal view. 103. Ventral view. 104. Dorsal view. 105. Lateral view. 106. Genital plates, caudoventral view. 107. Spermatheca. 108. Spermathecal pump.



Map 7. *T. cubensis* (■); *T. obsoleta* (★); *T. testacea* (●).

*Diagnosis.* Dorsal coloration brown to green; transhumeral reddish markings lacking.

Lateral jugal margins sinuous, not parallel (Fig. 94). Anterolateral margins of pronotum slightly concave in dorsal view, usually contrastingly pale yellow; humeral angles spinose with spines small and directed anterolaterad (Fig. 93); pronotal cicatrices immaculate. Abdominal sternites with anterolateral angles immaculate, posterolateral angles piceous. Postspiracular black spot present on each side of each abdominal sternite.

Basal plates in caudoventral view with mesial margins straight to slightly convex; posterior margins sinuous; posteromesial angles broadly rounded (Fig. 106). Pygophoral opening subtended by semicircular impression in caudal view; posterior margin of pygophore produced posterodorsad, convex with small, medial, V-shaped emargination in both ventral and dorsal views (Figs. 103, 104); pygophore slightly concave in lateral view (Fig. 105).

*Types.* Barber and Bruner (1932) described *Thyanta cubensis* from 14♂♂ and 5♀♀ specimens, all from Cuba. The holotype and 11 paratypes were examined. The holotype is housed in the U.S. National Museum of Natural History (Washington, D.C.).

*Distribution.* Bahama Islands and Cuba (Map 7).

*Specimens examined.* 32 specimens collected during every month except January, May, June, and November; deposited in AMNH, CAS, ISU, LHR, MSU, USNM. BAHAMA ISLANDS: Andros Island: Mangrove Bay. Cat Island. CUBA: Boniato. Archipiélago de los Canarreos: Isla de Pines. Camagüey: Camagüey. Ciego de Avila: Baraguá. Cienfuegos: Soldad near Cienfuegos. Granma: Cayamas. Pinar del Río:

Sierra Rangel. *Sancti Spíritus*: Zaza del Medio. *Santiago de Cuba*: Santiago de Cuba. *Villa Clara*: Santa Clara.

*Comments.* *Thyanta cubensis* is often smaller than the other species related to *T. perditior*, the humeral spines are shorter, the transhumeral reddish markings are usually absent, and the pronotal and abdominal black markings are reduced or absent.

*Thyanta (Thyanta) serratulata* Ruckes  
Figs. 109–121

*Thyanta serratulata* Ruckes, 1957c:178–179, figs. 5–6.

*Diagnosis.* Body shape broad, stout.

Lateral jugal margins sinuous, not parallel (Fig. 110). Anterolateral pronotal margins immaculate, in dorsal view concave, serrate, especially anteriorly; humeral angles spinose, spines relatively short, directed anterolaterad (Fig. 109). Pronotal cicatrices immaculate or often marked with black in each mesial angle. Postspiracular black spots absent. Anterolateral angles of abdominal sternites immaculate; posterolateral abdominal angles concolorous with rest of segment or sometimes marked with black.

Basal plates in caudoventral view with mesial margins straight to slightly convex; posterior margins sinuous (Fig. 116). Pygophoral opening subtended by semicircular impression; posterior margin of pygophore produced posterodorsad, convex with small, medial, V-shaped emargination in caudal view (Fig. 114); slightly concave in lateral view (Fig. 115).

*Types.* Ruckes (1957c) described *T. serratulata* from 13♂♂ and 13♀♀ specimens. The holotype and 17 paratypes were examined. The holotype is housed in the California Academy of Sciences (San Francisco).

*Distribution.* Known only from the type locality: Clarión Island, Revillagigedo Islands, Mexico.

*Specimens examined.* 21 specimens collected between 27 February and 8 May; deposited in AMNH, CAS, LACM, USNM. MÉXICO: Colima: Revillagigedo Islands, Clarión Island.

*Comments.* *Thyanta serratulata* can be identified by the broad, stout shape, the short humeral spine, the lack of post-spiracular black spots, and the reduction or absence of black markings on the lateral abdominal angles.

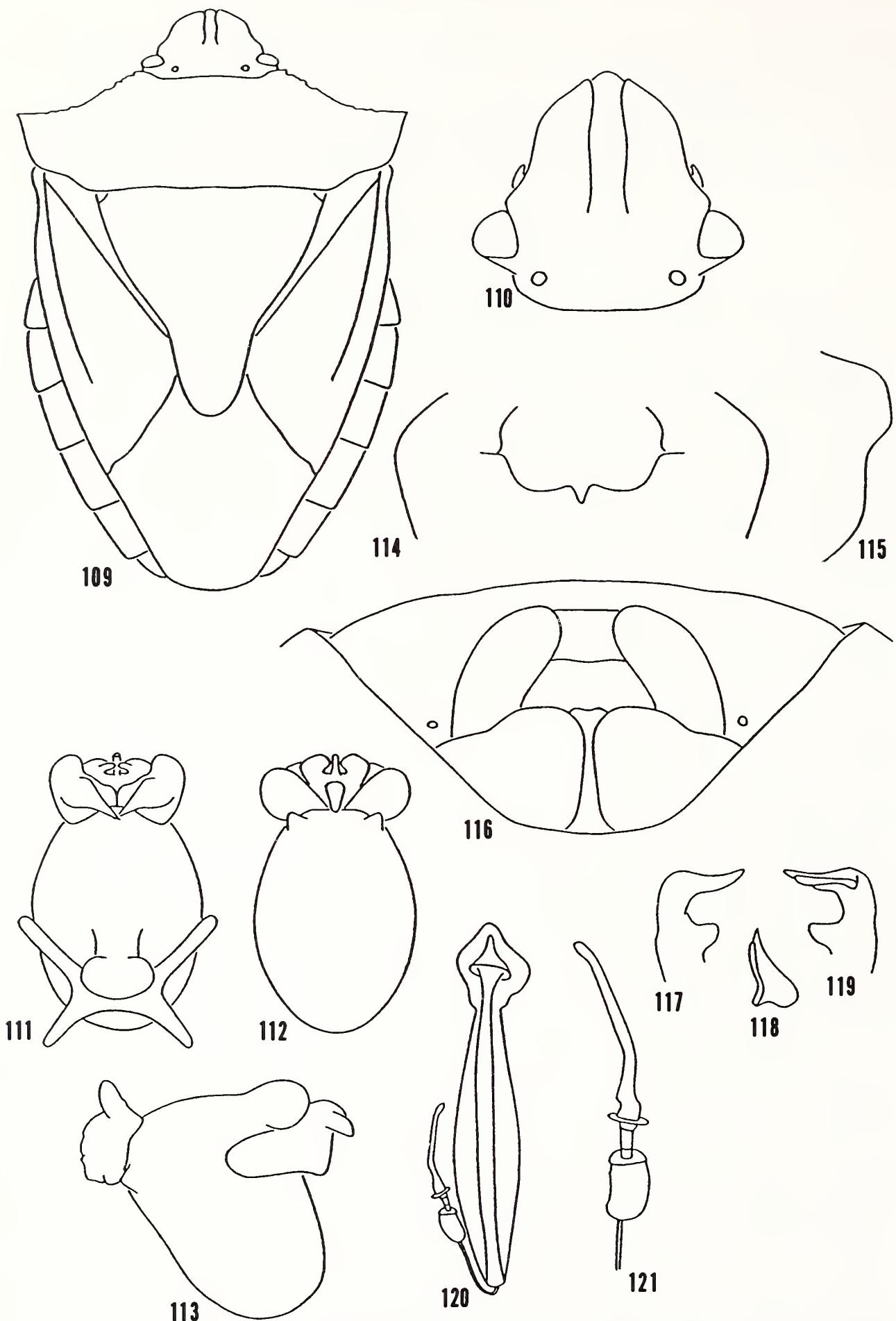
Subgenus *Argosoma* Rider

*Thyanta (Argosoma)* Rider [in Rider and Chapin, 1991:33].

*Type species.* *Pentatoma patruelis* Stål, 1859 (by original designation, Rider and Chapin, 1991).

*Diagnosis.* Punctuation coarse, sparse, dorsal surface appearing glossy. Anterolateral margins of pronotum straight to slightly concave, concolorous with surface of pronotum; humeral angles rounded to angulate, rarely spinose; pronotal cicatrices usually immaculate, sometimes faintly marked with fuscous in mesial angles. Posterior termination of each buccula evanescent.

Distal end of sclerotized rod with or without subapical swelling, never cone-shaped; spermathecal bulb globose; spermathecal duct below proximal flange slightly to greatly swollen and coiled, but never forming distinct cylindrical structure. Pygophoral



Figs. 109–121. *T. serratulata*. 109. Habitus. 110. Head. 111–113. Theca and related structures. 111. Ventral view. 112. Dorsal view. 113. Lateral view. 114, 115. Pygophore. 114. Caudal view. 115. Lateral view. 116. Genital plates, caudoventral view. 117–119. Right paramere. 117. Medial view. 118. Ectal view. 119. Lateral view. 120. Spermatheca. 121. Spermathecal pump.

opening relatively large; posterior margin usually broadly and shallowly U-shaped; posteroventral surface of pygophore produced into blunt chin-like protuberance. Each paramere acute to narrowly rounded apically, obtuse protuberance on shaft moderate in size to absent, possessing distinct dorsomedial concave surface; roughened, spiculate area on lateral surface of paramere usually circular, rarely linear (*T. boliviensis* Rider). Theca reniform, lacking dorsolateral protuberances; each lateral conjunctival lobe usually with single diverticulum; median penial lobes and penisfilum usually relatively small.

**Comments.** This is the largest subgenus, containing 20 species, and the included species are also the most difficult to identify. It is often necessary to examine the male genitalia in order to make accurate determinations. Within geographical areas, the internal female genitalia are usually distinctive.

This subgenus can be divided into two groups based primarily on the structure of the spermatheca. In *T. boliviensis*, *T. brasiliensis* Jensen-Haarup, *T. emarginata* Rider, and *T. hamulata* Rider, the sclerotized rod is somewhat elongate and lacks any subapical swelling. The remaining species have the sclerotized rod shorter and distinctly swollen subapically, becoming narrowed apically.

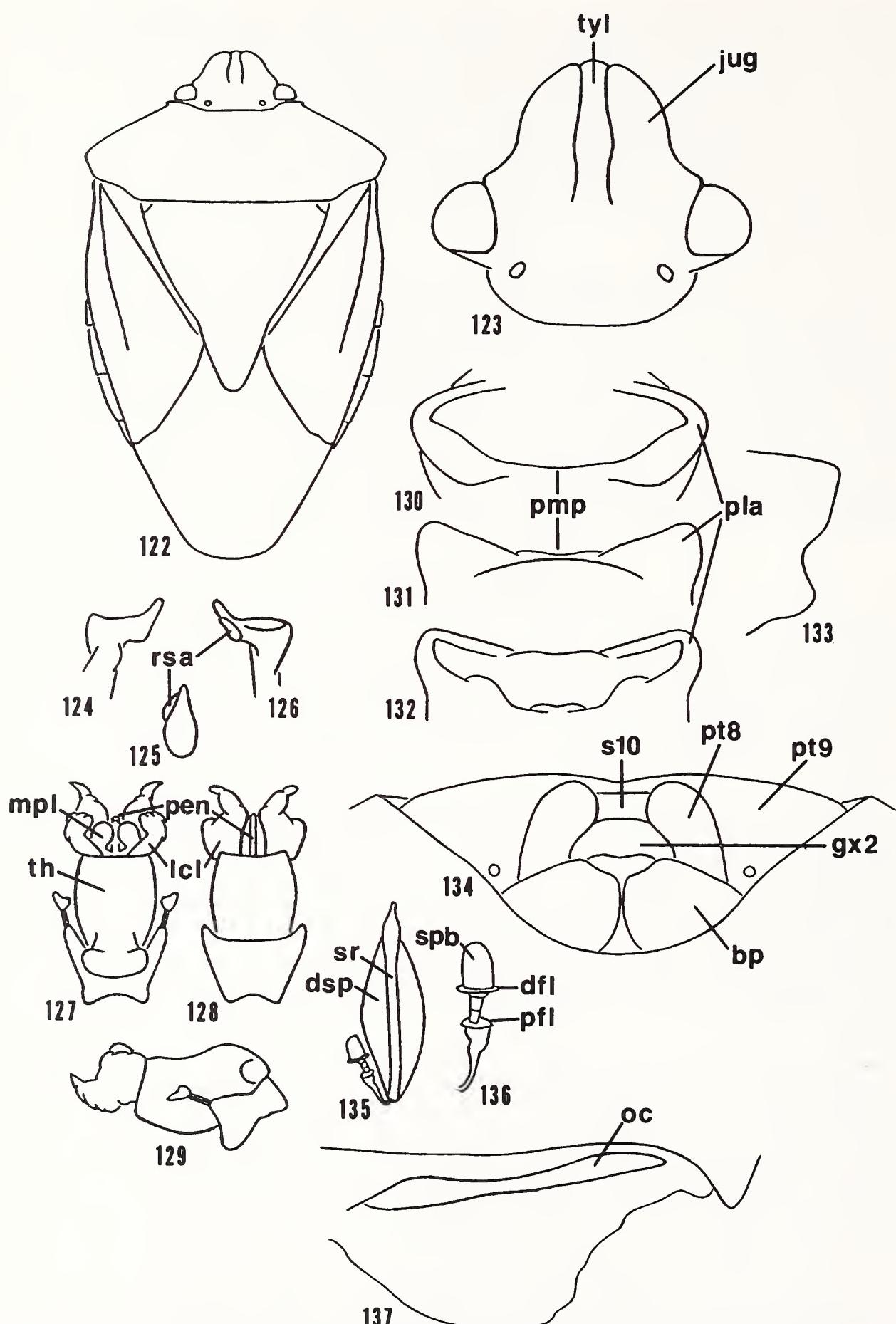
*Thyanta (Argosoma) planifrons* Ruckes  
Figs. 122–137, Map 6

*Thyanta planifrons* Ruckes, 1956:59–61, fig. 3; Rolston and McDonald, 1984:fig. 33. *Thyanta casta* (of authors, not Stål): Uhler, 1894a:231 (part); Van Duzee, 1904:52, 54 (part); Kirkaldy, 1909:94 (part); Banks, 1910:90; Van Duzee, 1917:53 (part); Van Duzee, 1923:127–128; Torre-Bueno, 1939:231 (part); Froeschner, 1988:593 (part).

**Diagnosis.** Vertex of head relatively flat; lateral jugal margins subparallel for middle third of distance from eyes to apex (Fig. 123). Anterolateral margins of pronotum straight to slightly concave in dorsal view; humeral angles rounded, not or only slightly produced beyond base of adjacent corium (Fig. 122). Pronotal cicatrices immaculate. Rarely with reddish markings on pronotum. Ostiolar canal widening towards apex, wider distally than in middle (Fig. 137). Abdominal sternites lacking black markings, rarely extreme tip of posterolateral angles of abdominal sternites piceous.

Basal plates with mesial margins slightly convex in caudoventral view, separated basally; posterior margins slightly convex; posteromesial angles rounded to slightly emarginate (Fig. 134). Sclerotized rod slightly swollen subapically, narrowed apically (Fig. 135); spermathecal duct only slightly swollen below proximal flange (Fig. 136). Posterior margin of pygophore broadly and shallowly U-shaped in caudal view, slightly sinuous medially (Fig. 130); posterior margin weakly concave in ventral and dorsal views (Figs. 131, 132); posteroventral surface deeply emarginate in lateral view (Fig. 133). Apex of each paramere nearly acute from both medial and ectal views (Figs. 124, 125); concave surface oriented more dorsad than mediad; roughened spiculate area on lateral surface elongate-circular (Fig. 126). Each lateral conjunctival lobe of aedeagus with 1 or 2 non-sclerotized diverticula (Fig. 129); dorsomedial lobe apparently absent (Fig. 128); median penial lobes spatulate (Fig. 127).

**Types.** Ruckes (1956) described *T. planifrons* from 6♂♂ and 7♀♀ specimens. The



Figs. 122-137. *T. planifrons*. 122. Habitus. 123. Head. 124-126. Right paramere. 124. Medial view. 125. Ectal view. 126. Lateral view. 127-129. Theca and related structures. 127. Ventral view. 128. Dorsal view. 129. Lateral view. 130-133. Pygophore. 130. Caudal view. 131. Ventral view. 132. Dorsal view. 133. Lateral view. 134. Genital plates, caudoventral view. 135. 136. 137.

holotype, which is from 10 miles west of Alamos, Sonora, Mexico, and all 12 paratypes were examined. The holotype is housed in the American Museum of Natural History (New York).

*Distribution.* Southwestern U.S. and northwestern Mexico (Map 6).

*Specimens examined.* 535 specimens collected during every month except February; deposited in AMNH, ASUT, CAS, DAR, DBT, EGER, FSCA, LACM, LHR, MSU, TAMU, UAT, UCB, UCR, UIM, UMC, UNAM, USNM. UNITED STATES: Arizona: *Cochise*: Portal; 5 mi W Portal, SWRS. *Pima*: Baboquivari Mountains, Browns Canyon; Organ Pipe Cactus Natl Monument. *Santa Cruz*: Madera Canyon. California: Imperial. *Riverside*: Bautista Canyon; Deep Canyon; Palm Springs. *San Diego*: Borego Valley.

MÉXICO: Canipole; 10 mi SW Canipole; Carmen Island, Porto Ballandra; Puntbunda. *Baja California Norte*: Bahía de los Angeles; Cataviña; 10 mi S Cataviña; 8 km N Punta Prieta; 15 mi N Punta Prieta; San Felipe; 12 mi S San Felipe; 15 mi S San Felipe; San Fernando. *Baja California Sur*: Bahía Concepción; Cabo San Lucas; 3 mi W Caduaño; Comondu; 10 mi SW Comondu; 20 mi N Comondu; 23 mi S Comondu; 14 mi S El Arco Mine; 28 mi S El Arco Mine; 6.5 mi S, 1 mi E El Pescadero; 15 mi N El Rufugio; El Sargento; El Triunfo; 2 mi NW El Triunfo; 6 mi N El Triunfo; Escondido Bay; 3 mi N Guajademi; Hamilton Ranch; 1 km SW Huatamote; Isla Annelvo; Isla Catalán; Isla Cerralvo; Isla Espírita Santo; La Paz; 2 mi S La Paz; 5 mi SW La Paz; 7 mi SW La Paz; 13 mi W La Paz; 14 mi W La Paz; 15 mi W La Paz; 20 mi NW La Paz; 21 mi W La Paz; 23 km W La Paz; 25 mi W La Paz; 26 mi W La Paz; 33.5 km NW La Paz; La Purisima; Las Animas; Las Barracas; Las Tinajitas; 2 mi SE Las Virgenes; 1 mi E Migriño; Miraflores; 5 mi S Miraflores; 4 mi S Mission San Javier; Mulegé; 1 mi S Mulegé; 2 mi S Rancho de la Ventana; 2.6 mi E San Antonio; 3 mi SW San Antonio; 5 mi S San Antonio; 5 mi W San Bartolo; San Domingo; 15 mi S San Domingo; 15 mi N San Ignacio; 27 mi W San Ignacio; San José del Cabo; 2 km W San José del Cabo; 10 mi SW San José del Cabo; 1.3 mi N San José Viejo; 3 mi N San José Viejo; 5 mi S San Miguel; 3 km S, 1.3 km E San Pedro; 3.5 mi NE San Pedro; San Sebastian; 5 mi SE Santa Rosalía; 12 mi S Santa Rosalía; Santiago; 6 mi SW Santiago; Sierra de la Laguna; Todos Santos; 4 mi N Todos Santos; 28–29 km N Todos Santos; Venancio; 30 mi E V. Insurgentes. *Sinaloa*: Mazatlán; 34 mi N Mazatlán. *Sonora*: 10 mi W Alamos; Bahía de los San Carlos; Bahía Kino; 20 mi NNE Ciudad Obregón; El Desemboque; Guaymas, Punta San Antonio; Hermosillo; La Choya; Minas Nuevas; 15 km S Navojoa; 15 mi N Navojoa; San Bernardino, Río Mayo; 20 mi S Sonoyta; Tecoripa; Tiburón Island; Yavaros.

*Comments.* *Thyanta planifrons* can be separated from all other congeners by the distal widening of the ostiolar canal. Also, the vertex of the head is relatively flat, a character for which this species was named.

←

135. Spermatheca. 136. Spermathecal pump. 137. Ostiolar canal. Symbols: bp, basal plate; dfl, distal flange; dsp, dilation of spermatheca: gx2, second gonacoxae; jug, juga; lcl, lateral conjunctival lobe; mpl, median penial lobe; oc, ostiolar canal; pen, penisfilum; pfl, proximal flange; pla, posterolateral angle of pygophore; pmp, posterior margin of pygophore; pt8, eighth paratergite; pt9, ninth paratergite; rsa, roughened spiculate area on lateral surface of paramere; spb, spermathecal bulb; sr, sclerotized rod; s10, tenth sternite; th, theca; tyl, tylus.

The widening of the ostiolar canal is unusual, but not unique. It also occurs in *Tepa jugosa* Van Duzee, a species with essentially the same distribution as *Thyanta planifrons*. The biological significance of this condition is not known, but would make an interesting study. This is the first record of this species from the United States.

*Thyanta (Argosoma) maculata* (Fabricius)  
Figs. 138–152, Map 8

*Cimex maculatus* Fabricius, 1775:704.

*Thyanta casta* Stål, 1862b:104; Stål, 1872:35; Uhler, 1876:7; Distant, 1880:66; Uhler, 1886:7; Uhler, 1894a:231 (part); Lethierry and Severin, 1893:147; Kirkaldy, 1909:94 (part); Malloch, 1919:217, fig. 74; Torre-Bueno, 1939:231 (part); Froeschner, 1988:593 (part). **NEW SYNONYMY.**

*Euschistus castus*: Walker, 1867:244.

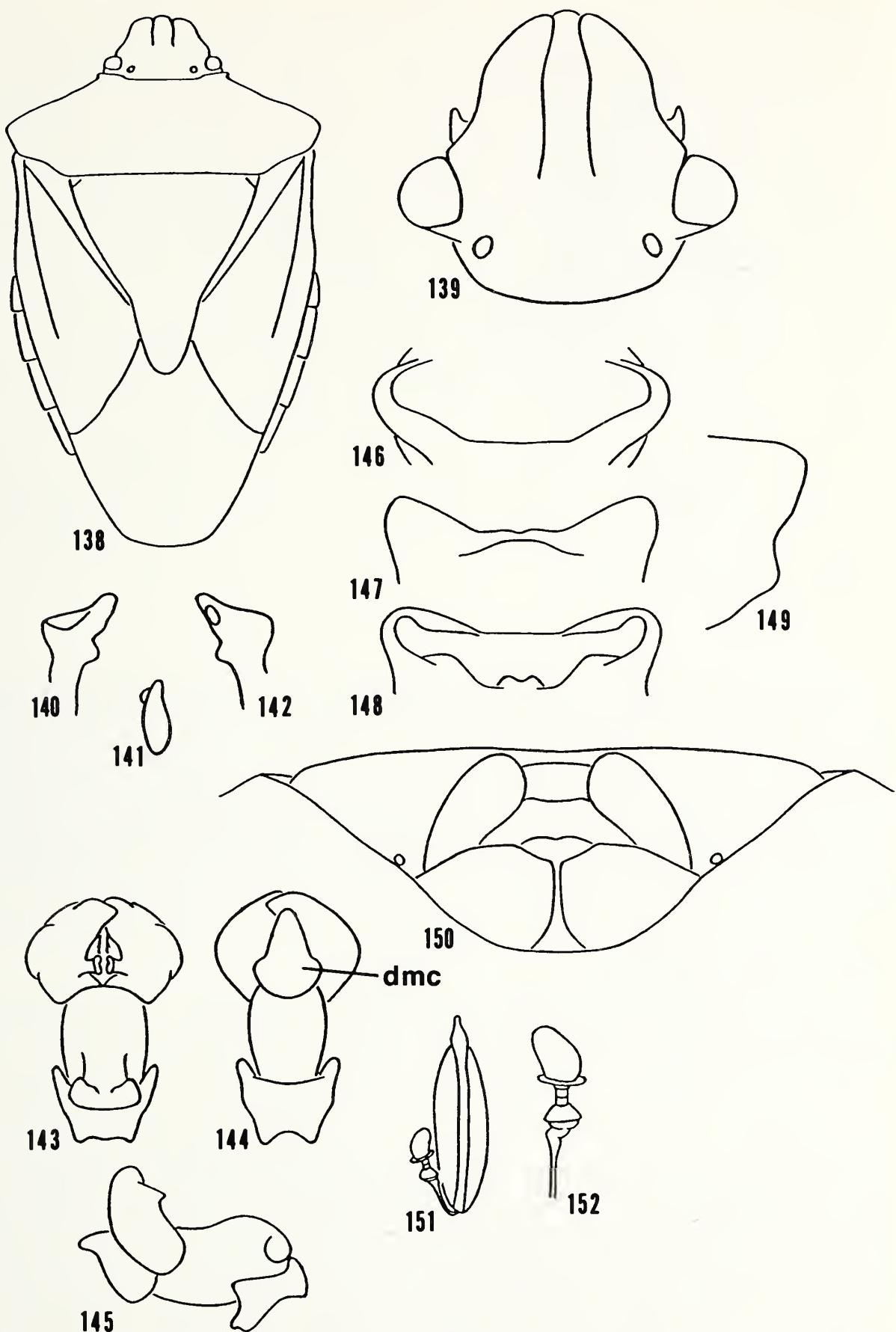
*Thyanta maculata*: Stål, 1872:35; Distant, 1893:334; Lethierry and Severin, 1893:148; Kirkaldy, 1909:94; Rolston and McDonald, 1984:fig. 29.

**Diagnosis.** General color green to brown; often with varying amounts of reddish on pronotum between humeral angles, often forming two oblong spots, one on each side of middle. Apices of scutellum and coria occasionally rubiginous.

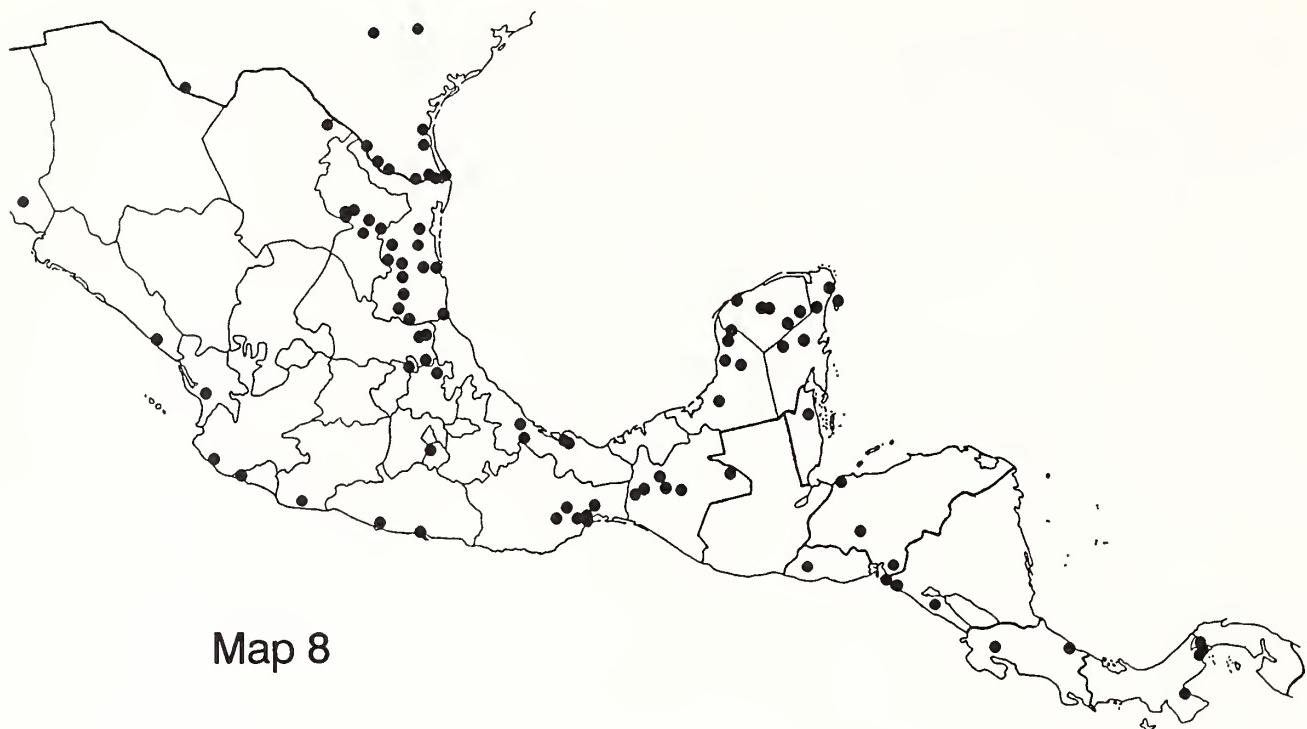
Lateral jugal margins sinuous, not quite parallel (Fig. 139). Anterolateral margins of pronotum nearly straight in dorsal view; humeral angles rounded to angulate, usually produced beyond base of adjacent corium by less than half width of eye (Fig. 138); pronotal cicatrices immaculate. Ostiolar canals acuminate apically. Postero-lateral angles of abdominal sternites piceous, sometimes only minutely so. Postspiracular spots usually absent, though sometimes present in brown form.

Basal plates with mesial margins slightly convex in caudoventral view, separated basally; posterior margins convex; posteromesial angles slightly emarginate (Fig. 150). Sclerotized rod swollen subapically, narrowed apically (Fig. 151); spermathecal duct moderately swollen and coiled below proximal flange (Fig. 152). Posterior margin of pygophore broadly and shallowly U-shaped in caudal view (Fig. 146); lateral angles prominent in ventral and dorsal views, chin-like protuberance relatively small (Figs. 147, 148); emarginate below middle in lateral view (Fig. 149). Apex of each paramere obtusely rounded in ectal view (Fig. 141); concave surface oriented more mediad than dorsad, shaft rather robust with small medial protuberance (Fig. 140); roughened spiculate area on lateral surface circular (Fig. 142). Aedeagus with lateral and dorsomedial conjunctival lobes large (Fig. 144), each lateral lobe with single, slightly sclerotized diverticulum (Fig. 143); penisfilum and median penial lobes obscured by conjunctiva (Fig. 145).

**Types.** Fabricius (1775) described *Cimex maculatus* from "America" without designating a holotype or paratypes. It is not possible to determine from his original description how many specimens he examined, but evidently he had more than one, as he mentions a variation. Only one syntype was located and examined. It is a ♀ in poor condition (apex of abdomen destroyed, left forewing missing, etc.), but it does possess the characters that define this species. It has the following label data: (a) "maculatus" (b) "Thyanta maculata F." and is here designated the lectotype. This specimen is housed in the Universitetets Zoologiske Museum (Copenhagen, Denmark).



Figs. 138–152. *T. maculata*. 138. Habitus. 139. Head. 140–142. Right paramere. 140. Medial view. 141. Ectal view. 142. Lateral view. 143–145. Theca and related structures. 143. Ventral view. 144. Dorsal view. 145. Lateral view. 146–149. Pygophore. 146. Caudal view. 147. Ventral view. 148. Dorsal view. 149. Lateral view. 150. Genital plates, caudoventral view. 151. Spermatheca. 152. Spermathecal pump. Symbol: dmc, dorsomedial conjunctival lobe.



Map 8

Map 8. *T. maculata*.

Stål (1862b) described *T. casta* from Mexico without designating a holotype or paratypes. One syntype, a ♀, was located and examined. Although it lacks the reddish markings that many specimens of *T. maculata* possess, it differs structurally in no significant manner from *T. maculata*. Because it is not possible to determine the number of specimens upon which Stål's description was based, the syntype specimen is designated the lectotype. It is labeled as follows: (a) "Mexico Coll. Signoret." (b) "Casta det. Stal" (c) "TYPE" (d) "Coll. Nat.-Mus. Wien" (e) "Thyanta casta STAL." The lectotype is housed in the Naturhistorisches Museum (Vienna, Austria).

*Distribution.* Southern Texas southward through Mexico and Central America to southern Panama (Map 8).

*Specimens examined.* 499 specimens collected during every month of the year; deposited in AMNH, ARH, BMNH, CAS, CNC, CUC, DAR, DBT, EGER, ENGL, FSCA, INHS, LACM, LHR, LSU, MSU, MSUE, OSU, OSUC, SMEK, TAMU, UAT, UCB, UCS, UGA, UMAA, UNAM, UNSM, UUSL. UNITED STATES: Texas: Brazos. *Burnet*: Inks Lake State Park. *Cameron*: Boca Chica; 3 mi SW Boca Chica; Brownsville; Harlingen; Sabal Palm Grove Sanctuary near Southmost. *Hidalgo*: Bentsen Rio Grande Valley State Park; Edinburg; McAllen; Progresso; Santa Ana Natl Wildlife Refuge. *Kleburg*: Kingsville. *Presidio*: Presidio. *San Patricio*: Corpus Christi Lake State Park; Nueces River, 5 mi SW Mathis. *Starr*: Falcon Heights; 4–15 mi N Roma. *Webb*: Laredo. *Zapata*: 1 mi E Falcon Lake; Falcon State Park.

MÉXICO: *Campeche*: Calkiní; 12 mi E Campeche; El Remate; Escárcega; Ruinas Edzna; km 54, Carr. Campeche-Merida. *Chiapas*: Aguacero, 16 km W Ocozocoautla; Chicoasen Dam Area; 13 mi W Cintalpa; 2 mi N Ocozcoautla; Ruinas Bonampak; San Cristóbal de las Casas; Santo Domingo, 15 mi SE Simojovel; Simojovel; Suchiapa. *Coahuila*: Arroyo de la Zorra. *Colima*: 2 mi N Manzanillo. *Guerrero*: Acapulco de Juárez; 3.7 mi E Marquelia; Tecpan de Galeana. *Hidalgo*: Otongo. *Jalisco*:

Chamela; Estacion de Biología Chamela. *Michoacán*: Acahuato. *Morelos*: 4.4 mi E Cuernavaca; Villa de Ayala. *Nayarit*: 15 km E San Blas. *Nuevo León*: Apodaca; 3 mi E Galeana; 16 mi S Linares, Anegade Arroyo; 4.1 mi S Montemorelos; Monterrey; 4 mi S Monterrey; 5 mi S Monterrey, Valle Alto; 6 mi S Monterrey. *Oaxaca*: 2.7 mi NW El Camaron; El Charquito; 6 mi W Jalapa del Marques; 8 mi N La Ventosa; Puerto Escondido; Salina Cruz; Tehuantepec; 11 mi W Tehuantepec; 12 mi W Tehuantepec; 13 km W Tehuantepec; 44 mi W Tehuantepec; 2.1 mi NW Totolapán. *Querétaro*: 1 mi NW Ayutla. *Quintana Roo*: 1 km N Coba; 20 km N Felipe Carrillo Puerto; 54 mi SE Peto; San Isidro Puerto Morelos; 2 mi NE San Miguel; River El Ramonal; Rancho El 24; Xcun Nuevo; km 146, Carr. Chetumal-Cancún; km 146, Carr. Chetumal-Pto Juarez. *San Luis Potosí*: 12 mi S Ciudad Mante; Ciudad Valles; 11 km E Ciudad Valles; El Banito; El Salto Falls; Tamazunchale; 5 mi N Tamazunchale; 30 mi S Tamazunchale; Tamuín. *Sinaloa*: 1 mi NW El Venadillo; Mazatlán; 5 mi N Mazatlán; 10 mi S Mazatlán; Presidio River near Caton. *Sonora*: 7 mi W Alamos. *Tamaulipas*: Abasolo; Antiguo Morelos; Bocatoma, Ciudad Victoria; 6 mi S Ciudad Victoria; 25 mi S Ciudad Victoria; 5 mi SSE Gómez Fariás; 6 mi S Gómez Fariás; Guemes; Hidalgo; 8 mi N Jiménez; La Pesca; Llera; 5 mi N Llera; 13 km E Magiscatzin; Punta Piedras; Río Corona, 30 km N Ciudad Victoria; San Fernando; 6.2 mi S San Fernando; 25 mi SE San Fernando; Tampico; Villagran. *Veracruz*: Córdoba; Cotaxtla; Cotaxtla Expt Stn; Cuitlahuac; Lake Catemaco Area; Ojo de Agui; Puente Nacionale; San Andres Tuxtla; 5 mi S Santiago Tuxtla; Tolome; 10 mi W Veracruz. *Yucatan*: Chichén Itzá; Piste; Progreso; 12 km N Quintana Roo, Hwy 295; 13 mi E Valladolid; 13.3 mi S Valladolid; 1 km S Xcalacoop; 10 km N Xcalacoop.

BELIZE: *Belize*: 12 mi NW Belize City. EL SALVADOR: Ruinas San Andres. HONDURAS: Choluteca. *Comayagua*: 5 mi NW Comayagua. *Cortes*: Puerto Cortés. NICARAGUA: Chinandega; N side Cosgóina Volcano, Gulf of Fonseca. *Managua*: Jiloa; Masachapa. COSTA RICA: Limón. *Guanacaste*: La Pacifica, near Cañas. PANAMA: Chitré; La Chorrera. *Canal Zone*: Barro Colorado Island; Base of Cerro Galera. DARIEN: Santa Fe.

*Comments.* *Thyanta maculata* was originally distinguished from other congeners by the presence of two oblong reddish macules, one on each side of the middle of the pronotum. Fewer than half the specimens of *T. maculata* actually exhibit this character. Also, several other species of *Thyanta* are known to have the same type of maculation in at least some specimens (*T. pseudocasta* Blatchley, *T. brasiliensis* Jensen-Haarup, *T. curvata* Rider).

*Thyanta maculata* can be separated from other congeners except *T. pseudocasta* by the structure of the male genitalia. Each paramere is rather robust with the apex rounded, and the dorsomedial concave surface is oriented more mediad than dorsad. *Thyanta pseudocasta* has very similar male genitalia, but the aedeagus is slightly different. The aedeagus of *T. maculata* has a dorsomedial conjunctival lobe, while the same structure is apparently absent in *T. pseudocasta*. The two forms can usually be separated based upon the prominence of the humeral angles. Each humeral angle in *T. maculata* is usually produced beyond the base of the adjacent corium by less than half the width of an eye, while in *T. pseudocasta* each humeral angle usually protrudes beyond the corium by more than half the width of an eye.

*Thyanta maculata* is a variable species, especially with respect to size and coloration. For example, specimens from the Yucatan peninsula of Mexico average much

smaller than specimens from other parts of the range, but they do not differ in any other significant manner.

*Thyanta (Argosoma) vadosa* Rider  
Figs. 153–167

*Thyanta (Argosoma) vadosa* Rider [in Rider and Chapin, 1991:55].

**Diagnosis.** Ovate; dorsal surface green to pale brown; some interstitial areas of pronotum, scutellum, and elytra pale yellow; sometimes marked with reddish-purple between humeral angles, on apex of scutellum, and on tylus and vertex of head. Punctures green to pale brown.

Apex of head arcuately rounded; lateral jugal margins sinuous, subparallel for middle third of distance from eyes to apex (Fig. 154); vertex convex. Anterolateral margins of pronotum in dorsal view straight to slightly concave; humeral angles rounded to angulate, often projecting beyond base of adjacent corium (Fig. 153). Pronotal cicatrices immaculate. Punctuation becoming sparse medially, central portion of pronotal disc subcalloused. Posterior third of pronotum often darker than rest of pronotum. Posterolateral angles of connexival segments piceous. Ostiolar canals acuminate apically. Postspiracular black spots usually absent (except in brown form); posterolateral angles of abdominal sternites piceous, sometimes only minutely so.

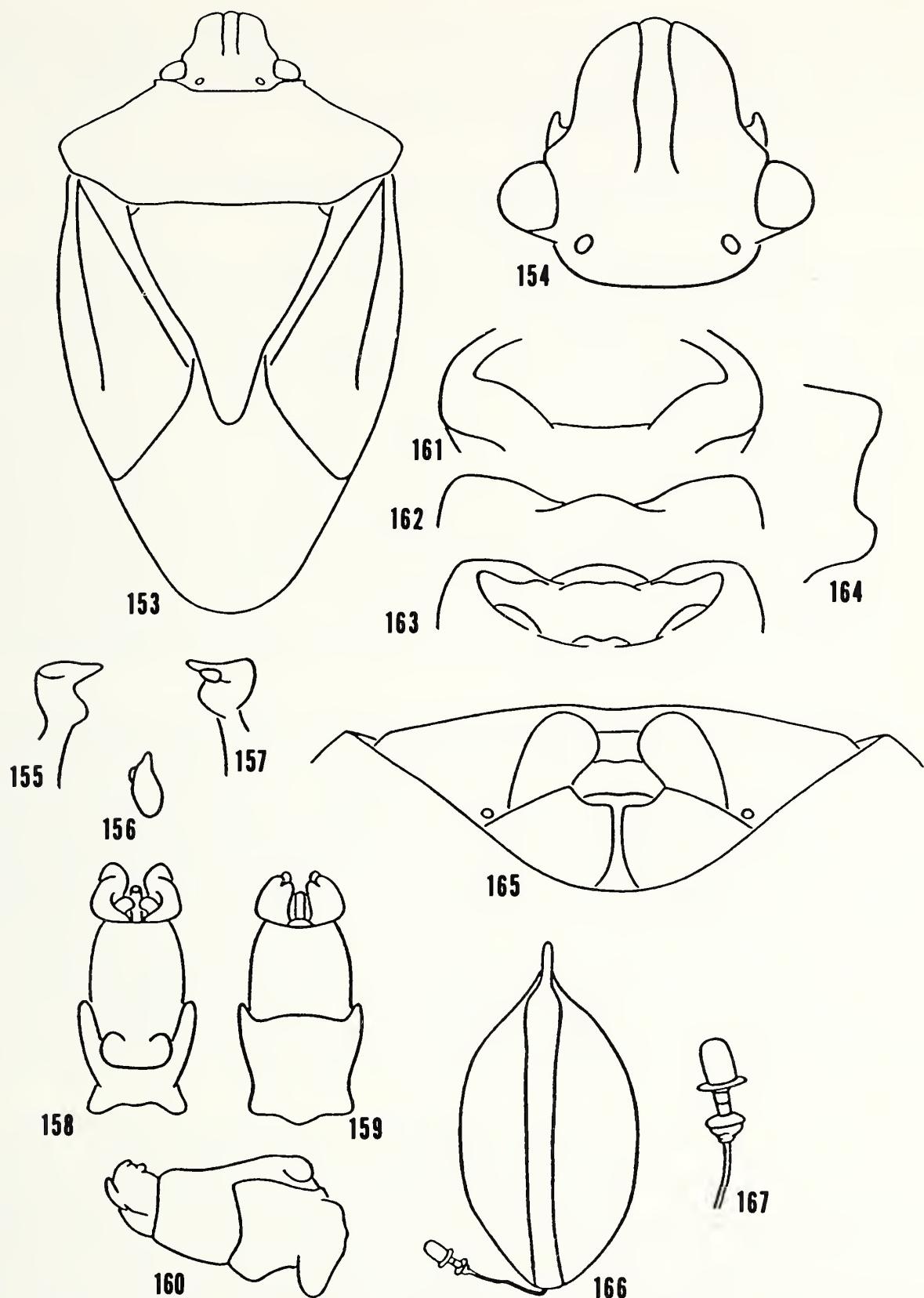
Mesial margins of basal plates straight to slightly convex in caudoventral view; posterior margins slightly convex; posteromesial angles broadly and shallowly emarginate, lateral sides of concavity resulting from excavations in basal plates divergent, not parallel (Fig. 165). Distal end of sclerotized rod swollen subapically, narrowed apically (Fig. 166); spermathecal duct moderately swollen and coiled below proximal flange (Fig. 167). Posterior margin of pygophore in caudal view broadly U-shaped, medial portion straight to slightly convex (Fig. 161); chin-like protuberance appearing relatively narrow in ventral and dorsal views (Figs. 162, 163); pygophore deeply emarginate in lateral view (Fig. 164). Each paramere with concave surface oriented mediad; from ectal view, parameral apex angling gently mesad (Fig. 156); from medial view, apex acutely angulate, straight or bending slightly ventrad (Fig. 155); roughened spiculate area on lateral surface circular (Fig. 157). Each lateral conjunctival lobe of aedeagus without sclerotized diverticula (Fig. 160); dorsomedial conjunctival lobe weakly developed (Fig. 159); median penial lobes spatulate (Fig. 158).

**Types.** Rider [in Rider and Chapin, 1991] described *T. vadosa* from 5♂♂ and 5♀♀ female specimens. The holotype ♂ was examined and is deposited in the Canadian National Collection, Ottawa, Canada.

**Distribution.** Trinidad and Tobago; Venezuela.

**Specimens examined.** 9 specimens collected in January, February, March, May, July, September, and October, deposited in AMNH, ARH, CNC, USNM. BRITISH WEST INDIES: Tobago. *Trinidad*: Bejucal; Curepe, Santa Margarita Circular Road; Saint Augustine; Santa Margarita Hill.

**Comments.** In general appearance this is a typical species of the *maculata* group. The shape of the emargination in the posteromesial angle of each basal plate of the female is distinctive. *Thyanta emarginata* and *T. excavata* both have the posteromesial angles of the basal plates deeply emarginate, but the sides of the resulting concavity are nearly parallel, not divergent as in *T. vadosa*. The male genitalia are



Figs. 153–167. *T. vadosa*. 153. Habitus. 154. Head. 155–157. Right paramere. 155. Medial view. 156. Ectal view. 157. Lateral view. 158–160. Theca and related structures. 158. Ventral view. 159. Dorsal view. 160. Lateral view. 161–164. Pygophore. 161. Caudal view. 162. Ventral view. 163. Dorsal view. 164. Lateral view. 165. Genital plates, caudoventral view. 166. Spermatheca. 167. Spermathecal pump.

also distinctive. *Thyanta vadosa* is the only species with the apex of each paramere not only acutely angulate (almost acuminate) but also straight or bending slightly ventrad. In the *maculata* group, all other species having the apex of each paramere acute to acuminate also have the apex bending dorsad.

*Thyanta (Argosoma) pseudocasta* Blatchley  
Figs. 168–182, Map 9

*Thyanta pseudocasta* Blatchley, 1926:114, 120; Blatchley, 1930:64; Torre-Bueno, 1939:230; Rolston and McDonald, 1984:figs. 26, 34; Froeschner, 1988:594.

*Thyanta casta* (of authors, not Stål): Barber, 1914:523; Van Duzee, 1917:53 (part); Torre-Bueno, 1939:231 (part); Froeschner, 1988:593 (part).

*Diagnosis.* General color pale green to pale brown, sometimes with anterior half of pronotum reddish.

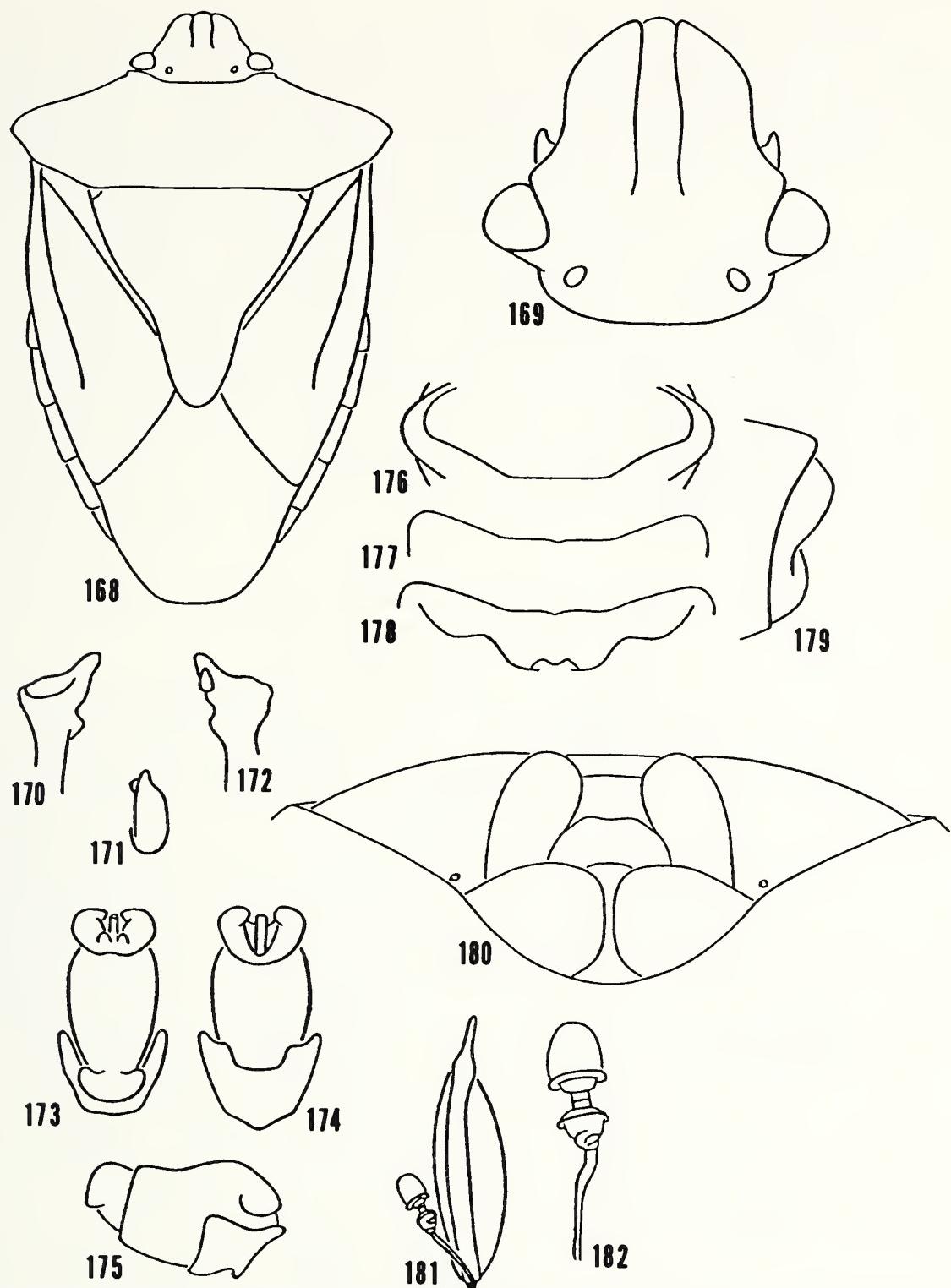
Lateral jugal margins subparallel for middle third of distance from eyes to apex (Fig. 169). Anterolateral margins of pronotum nearly straight in dorsal view; humeral angles prominent, produced beyond base of adjacent corium by more than half width of eye, rounded to angulate (Fig. 168). Pronotal cicatrices immaculate. Ostiolar canals acuminate apically. Posterolateral angles of abdominal sternites piceous, sometimes only minutely so. Postspiracular black spots usually absent, sometimes present in brown form.

Basal plates in caudoventral view with mesial margins straight to slightly convex; posterior margins evenly convex, posteromesial angles rounded (Fig. 180). Sclerotized rod slightly swollen subapically, narrowed apically (Fig. 181); spermathecal duct with small amount of swelling and coiling below proximal flange (Fig. 182). Posterior margin of pygophore in caudal view broadly and shallowly U-shaped, slightly sinuous medially in caudal, ventral, and dorsal views (Figs. 176–178); pygophore emarginate in lateral view (Fig. 179). Apex of each paramere from ectal view nearly acute (Fig. 171); from medial view narrowly rounded; concave surface facing mediad (Fig. 170); roughened spiculate area on lateral surface circular (Fig. 172). Aedeagus with each lateral conjunctival lobe apparently lacking sclerotized diverticula (Fig. 175); dorsomedial lobe apparently absent (Fig. 174); median penial lobes relatively small (Fig. 173).

*Types.* Blatchley (1926) described *T. pseudocasta* without designating a holotype or paratypes. In 1930, however, he designated 1♂ specimen as “type” (lectotype). He did not mention any of the other syntypes. Although actual paralectotype designations were not made, according to the International Code of Zoological Nomenclature (Ride et al., 1985, sect. 74a[iv]), once the lectotype is designated the remaining syntypes automatically become paralectotypes. Accordingly, no such designations are needed, but labels have been added to the specimens to indicate their actual status.

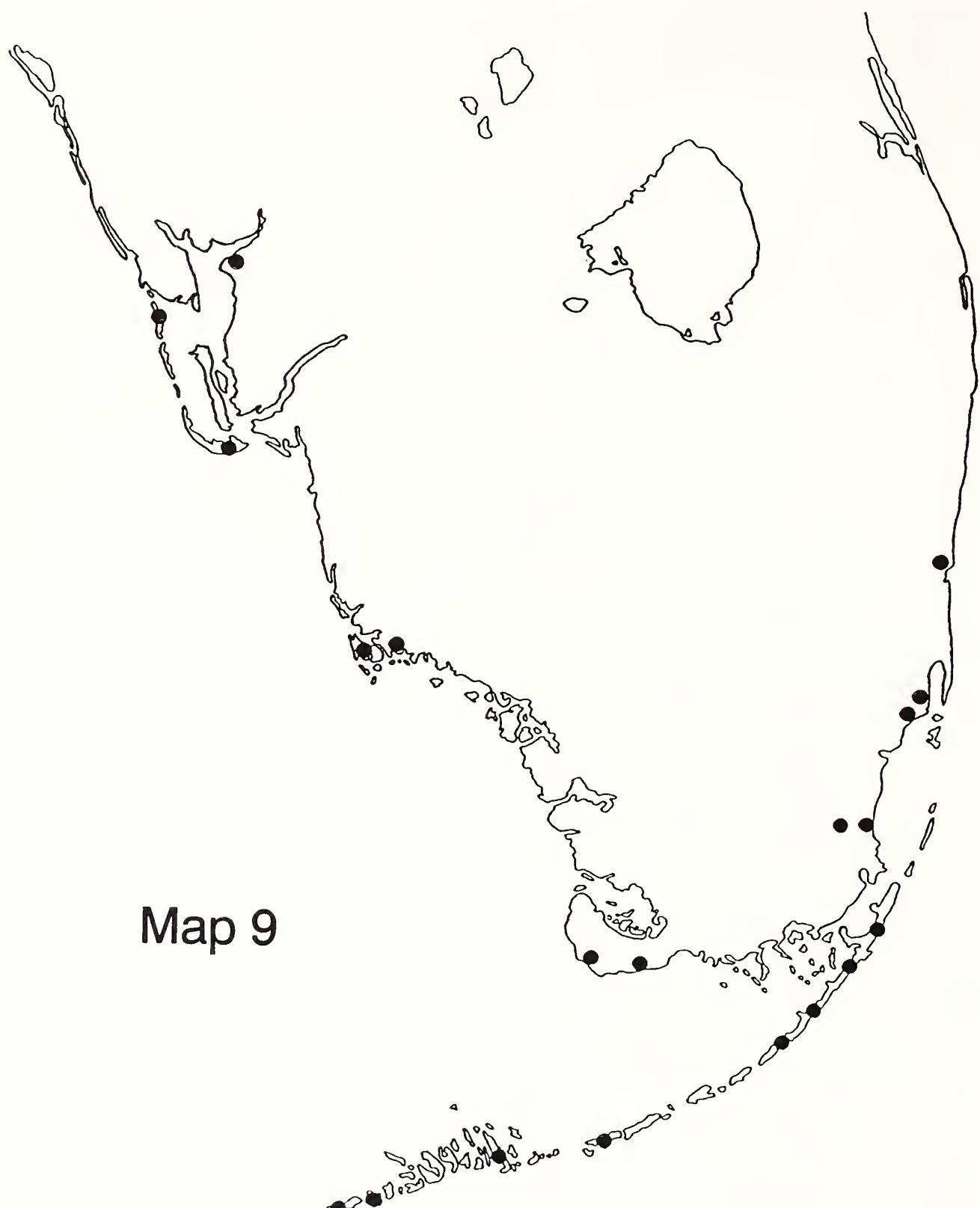
Regrettably, the ♂ lectotype is in deplorable condition; all that remains is the head and pronotum. It has the following label data: (a) “Miami Fla. W. S. B. Coll. 3-11-24” (b) “Purdue Blatchley collection” (c) “TYPE” (d) “*Thyanta pseudocasta* Blatchley.” The lectotype is deposited in the Purdue University Collection (W. Lafayette, IN).

Ten additional specimens that are believed to be part of the original syntype series



Figs. 168–182. *T. pseudocasta*. 168. Habitus. 169. Head. 170–172. Right paramere. 170. Medial view. 171. Ectal view. 172. Lateral view. 173–175. Theca and related structures. 173. Ventral view. 174. Dorsal view. 175. Lateral view. 176–179. Pygophore. 176. Caudal view. 177. Ventral view. 178. Dorsal view. 179. Lateral view. 180. Genital plates, caudoventral view. 181. Spermatheca. 182. Spermathecal pump.

have been located: 1♂ and 2♀♀ labeled (a) "Miami Fla. W. S. B. Coll. 3-11-24" (b) "Purdue Blatchley collection" (AMNH, PUL), except 1♀ labeled (c) "Thyanta pseudocasta Blatchley" (LSU); 3♂♂ and 2♀♀ labeled (a) "C. Sable Fla. W. S. B. Coll. 2-23-19" (b) "Purdue Blatchley collection" (PUL), except 1♂ labeled (b) "H G Barber Colln1950" (USNM), and 1♂ and 1♀ labeled "4-5-25" (AMNH); 1♂ labeled (a) "K.



Map 9

Map 9. *T. pseudocasta*.

West Fla. W. S. B. Coll. 3-2-19" (b) "Purdue Blatchley collection" (PUL); and 1♂ labeled (a) "Coxam Fla. W. S. B. Coll. 3-8-21" (b) "Purdue Blatchley collection" (LSU). The lectotype and all but one paralectotype were examined.

*Distribution.* Southern Florida (Map 9).

*Specimens examined.* 153 specimens collected during every month of the year; deposited in AMNH, ARH, CAS, CNC, CU, DAR, DBT, EGER, FSCA, LHR, LSU,

MSU, PUL, SMEK, UCB, UCS, UGA, UMC, USNM. UNITED STATES: Florida: Caxambus. *Broward*: Fort Lauderdale. *Charlotte*: Charlotte Harbor Area, Little Gasparillo Island; Punta Gorda. *Collier*: Marco Island; Royal Palm Park. *Dade*: Biscayne Bay; Coral Gables; Homestead; Miami. *Lee*: Sannibel Island. *Monroe*: Big Pine Key; Cape Sable; Everglades Natl Park; Key Largo; Key West; Marathon Key; Plantation Key; Stock Island; Tavernier Key; 9 mi NW Key Largo.

*Comments.* *Thyanta pseudocasta* can be separated from all congeners except *T. maculata* because the concave surface of its paramere is oriented more mediad than dorsad. *Thyanta pseudocasta* may actually be a subspecies of *T. maculata*. The male genitalia of the two species are very similar, but there are some differences in the aedeagus. *Thyanta maculata* has a prominent dorsomedial conjunctival lobe, while this structure is apparently absent in *T. pseudocasta*. Also, the humeral angles are more prominent in *T. pseudocasta*. Because these species represent reproductively isolated populations, a conservative approach is taken, and they are retained as full species.

*Thyanta (Argosoma) obsoleta* (Dallas)  
Figs. 183–197, Map 7

*Pentatoma obsoleta* Dallas, 1851:251; Walker, 1867:289.

*Thyanta obsoleta*: Lethierry and Severin, 1893:148; Kirkaldy, 1909:94.

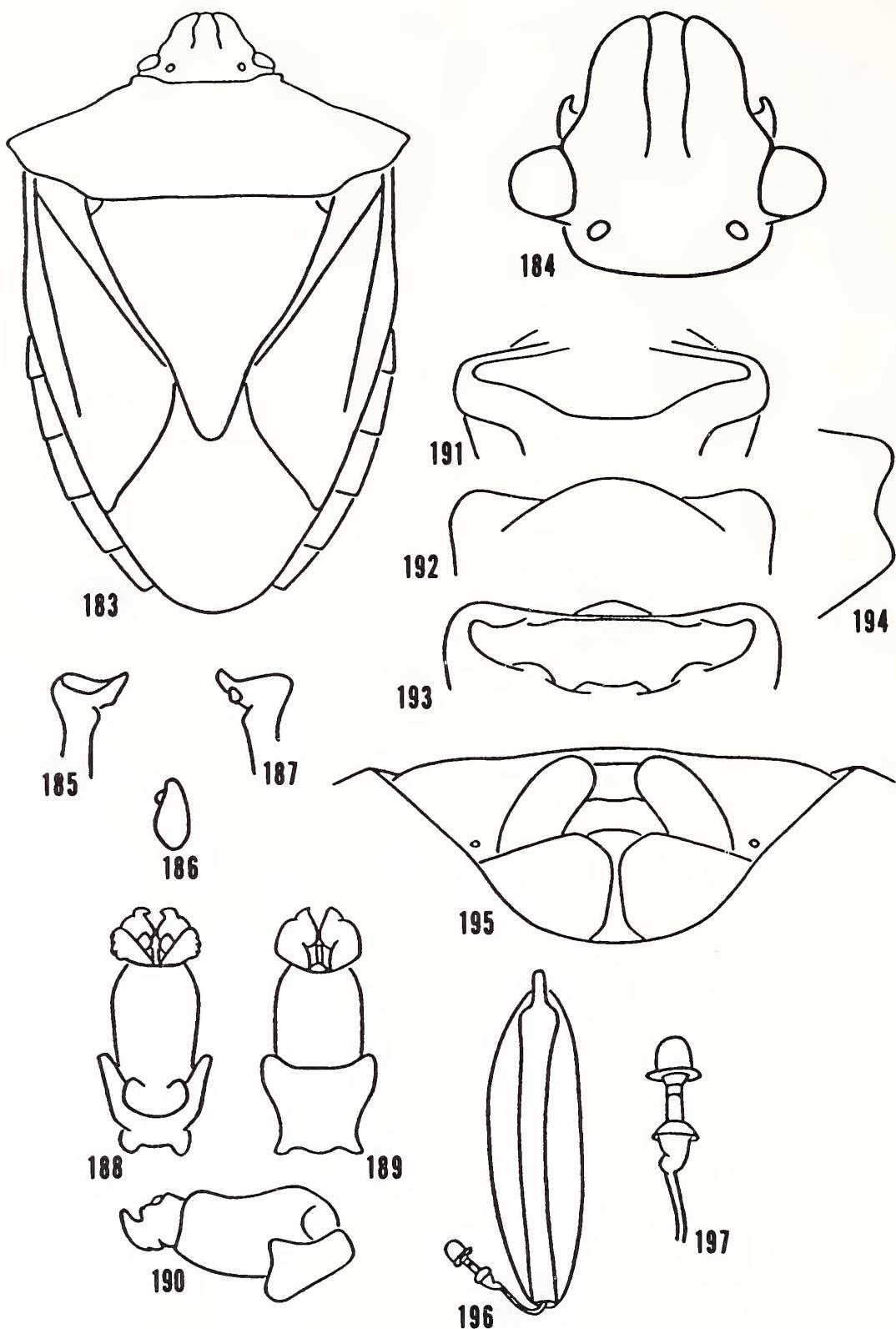
*Thyanta casta* (of authors, not Stål): Van Duzee, 1904:52, 54 (part); Kirkaldy, 1909: 94 (part); Barber, 1923:12; Barber, 1939:292–293.

*Diagnosis.* Coloration green to pale brown, often with transhumeral reddish markings that sometimes form two oblong spots, one each side of middle.

Lateral jugal margins subparallel for middle third of distance from eyes to apex (Fig. 184). Anterolateral margins of pronotum straight to slightly concave in dorsal view; humeral angles rounded to angulate, usually produced beyond base of adjacent corium by about half width of eye (Fig. 183). Pronotal cicatrices immaculate. Ostiolar canals acuminate apically. Posterolateral abdominal angles piceous; postspiracular black spots usually absent, sometimes evident in brown form.

Mesial margins of basal plates in caudoventral view straight to slightly convex; posterior margins slightly convex; posteromesial angles broadly rounded (Fig. 195). Sclerotized rod swollen subapically, narrowed apically (Fig. 196); spermathecal duct moderately swollen below proximal flange with only slight amount of coiling (Fig. 197). Posterior margin of pygophore broadly and shallowly U-shaped in caudal view (Fig. 191); in lateral view concave (Fig. 194); posterior margin only slightly concave in dorsal view, posterolateral angles not prominent (Fig. 193); posterovenentral surface distinctly produced into blunt chin-like protuberance in ventral view (Fig. 192). Each paramere apically rounded in ectal view (Fig. 186); narrowly rounded from medial view, curving dorsad; concave surface oriented more dorsad than mediad (Fig. 185); roughened spiculate area on lateral surface circular (Fig. 187). Each lateral conjunctival lobe of aedeagus with 1 or 2 subacute diverticula (Fig. 190), dorsomedial lobe reduced (Fig. 189); median penial lobes large, spatulate (Fig. 188); penisfilum reduced.

*Types.* Dallas (1851) described *Pentatoma obsoleta* from Jamaica without designating a holotype or paratypes, and it is not possible to determine the number of specimens upon which he based his description. Only 1♀ syntype was located, and



Figs. 183-197. *T. obsoleta*. 183. Habitus. 184. Head. 185-187. Right paramere. 185. Medial view. 186. Ectal view. 187. Lateral view. 188-190. Theca and related structures. 188. Ventral view. 189. Dorsal view. 190. Lateral view. 191-194. Pygophore. 191. Caudal view. 192. Ventral view. 193. Dorsal view. 194. Lateral view. 195. Genital plates, caudoventral view. 196. Spermatheca. 197. Spermathecal pump.

it is here designated the lectotype. It is labeled (a) "Jamaica" [dorsal surface], "45 1111" [ventral surface] (b) "Type" (c) "35. *Pentatoma obsoleta*." The lectotype, which is housed in the British Museum of Natural History (London), was examined.

*Distribution.* Greater Antilles (Map 7).

*Specimens examined.* 60 specimens collected during every month of the year except September; deposited in AMNH, ARH, BMNH, CAS, CNC, CU, DAR, DBT, ENGL, LHR, OSU, SMEK, UAT, USNM. BAHAMA ISLANDS: San Salvador Island. CUBA: *Ciudad de la Habana*: El Cano; Havana. *Guantánamo*: Guantánamo Bay Naval Base, Caravella Point. *Santiago de Cuba*: Daiquirí; Jarahueca. JAMAICA: Bluefields; Christiana; Mona, near Kingston; St. Andrew Ferry; Try. Duncans. *St. Andrew*: Bamboo Lodge near Irish Town. *Westmorland*: Negril, Negrillo Cottages. HAITI: Diquini. *Ouest*: Port-au-Prince. DOMINICAN REPUBLIC: Los Hidalgos; 8 mi up Macorís River, Santo Domingo. *Distrito Nacional*: La Victoria; Santo Domingo City. *Peravia*: 13 km NW Baní. *Samaná*: Sánchez. *San Cristóbal*. *San Juan*: 16 km SE San Juan; 28 km E San Juan. PUERTO RICO: Aguirre; Fortuna A.E.S. *Humacao*: Vieques Island, Puerto Real. *Mayagüez*: Guánica Forest, Hwy 334 at Ranger Station. *Ponce*: Coamo Springs; Ponce.

*Comments.* Examination of the male genitalia is necessary to separate this species from other species in the *maculata* group. *Thyanta obsoleta* can be distinguished from other Northern Hemisphere species by its apically rounded parameres, which have the concave surface oriented more dorsad than mediad.

*Thyanta (Argosoma) testacea* (Dallas)  
Figs. 198–212, Map 7

*Pentatoma testacea* Dallas, 1851:250; Walker, 1867:289.

*Thyanta testacea*: Stål, 1872:35; Berg, 1878:23, Lethierry and Severin, 1893:148; Kirkaldy, 1909:95.

*Thyanta casta* (of authors, not Stål): Uhler, 1893:705; Uhler, 1894b:174.

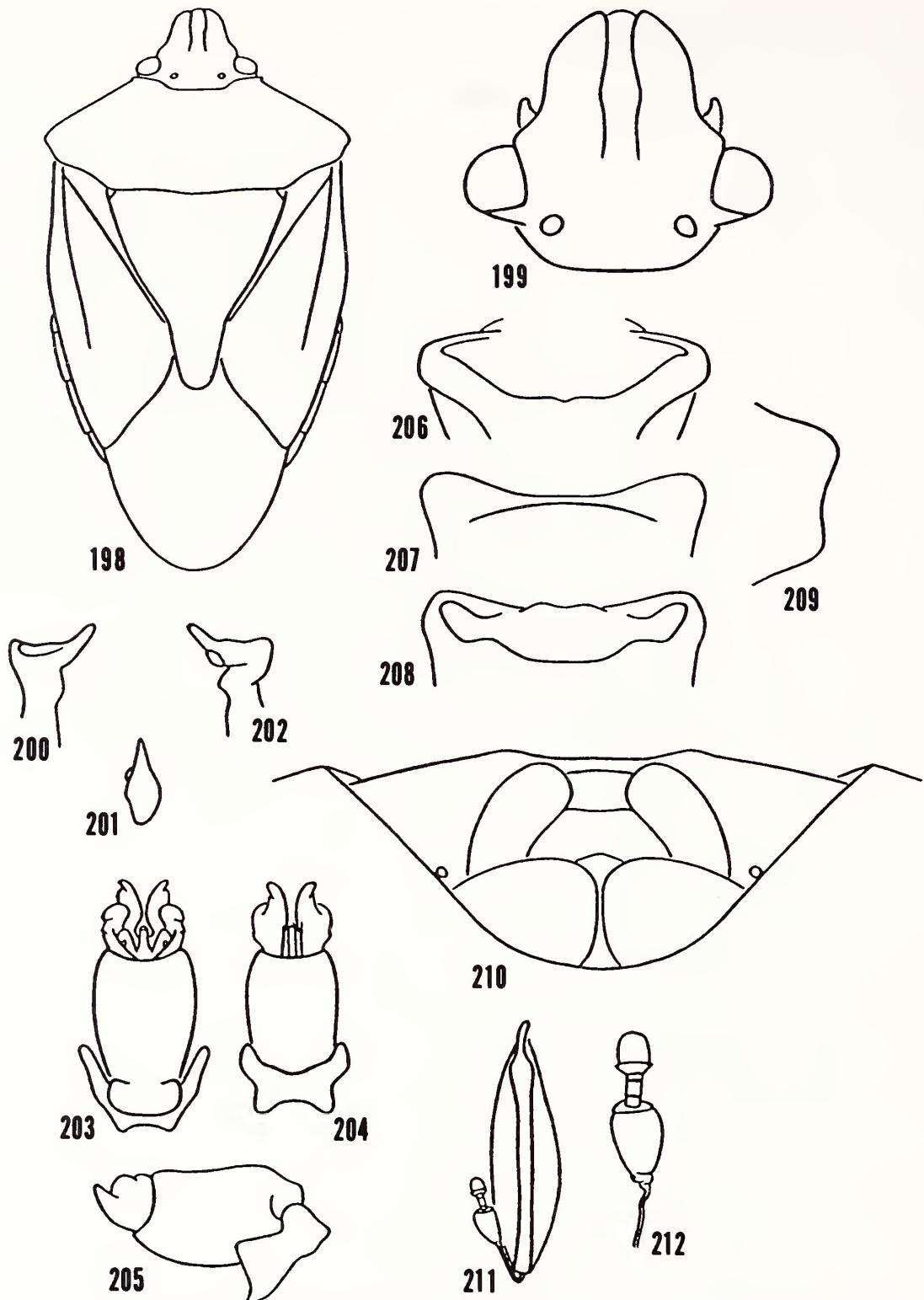
*Thyanta signoreti* Ruckes, 1956:65–66, fig. 7 (syn. by Rider and Chapin, 1991).

*Thyanta (Argosoma) testacea*: Rider and Chapin, 1991.

*Diagnosis.* General color green to brown, rarely with rubiginous transhumeral markings.

Lateral jugal margins subparallel for middle third of distance from eyes to apex (Fig. 199). Anterolateral pronotal margins straight to slightly concave; humeral angles angulate to rounded, usually produced beyond base of adjacent corium by about half width of eye (Fig. 198). Pronotal cicatrices immaculate. Ostiolar canals acuminate apically. Posterolateral abdominal angles not marked with black or only minutely so; postspiracular black spots usually absent, sometimes evident in brown form.

Basal plates in caudoventral view with mesial margins convex, separated basally; posterior margins convex (Fig. 210). Distal end of sclerotized rod slightly swollen subapically, narrowed apically (Fig. 211); spermathecal duct greatly swollen below proximal flange, carrot-shaped (Fig. 212). Posterior margin of pygophore broadly and shallowly U-shaped in caudal view (Fig. 206); slightly concave in lateral view (Fig. 209). Each paramere apically acute in both medial and ectal views (Figs. 200, 201); concave surface oriented more dorsad than mediad; roughened spiculate area



Figs. 198–212. *T. testacea*. 198. Habitus. 199. Head. 200–202. Right paramere. 200. Medial view. 201. Ectal view. 202. Lateral view. 203–205. Theca and related structures. 203. Ventral view. 204. Dorsal view. 205. Lateral view. 206–209. Pygophore. 206. Caudal view. 207. Ventral view. 208. Dorsal view. 209. Lateral view. 210. Genital plates, caudoventral view. 211. Spermatheca. 212. Spermathecal pump.

on lateral surface circular (Fig. 202). Aedeagus with dorsomedial lobe apparently absent (Fig. 204).

**Types.** Dallas (1851) described *Pentotoma testacea* from "S. America" without designating a holotype or paratypes, and it is not possible to determine how many

syntypes he had. Rider and Chapin (1991) designated the only known ♀ syntype as lectotype. The lectotype, which is conserved in the British Museum of Natural History (London), was examined.

*Distribution.* Lesser Antilles and northern South America (Map 7).

*Specimens examined.* 250 specimens collected during every month of the year, deposited in AMNH, ARH, BMNH, CAS, CU, DBT, EGER, ENGL, INHS, LACM, LHR, LSU, MSUE, SMEK, TAMU, USNM. BRITISH VIRGIN ISLANDS: *Tortola Island*. U.S. VIRGIN ISLANDS: *St. Croix*: Canaan; Christiansted; E Hill; Experiment Station Grounds; Hams Bluff. *St. John*: Estate Carolina, NW of Coral Bay; Virgin Islands Natl Park. *St. Thomas*: Charlotte Amalie; Estate Lilliendahl; Frenchman's Bay. BRITISH WEST INDIES: *Anguilla*: N of Road Bay. *Antigua*: Coolidge; Coolidge airport. *Bequia*. *Dominica*: Antrim; Cabrit Swamp; Clarke Hall; Grande Savane; Macoucheri; Mero Beach; Salybia; Springfield Estate; S Chiltern. *Grenada*: Caliveny Estate; Grand Anse, St. Georges Parish; Granville; Mt Gay Estate; St. Georges; Santeurs. *Montserrat*: Galway's Estate; Plymouth. *St. Kitts*: W Farm Gut. *St. Lucia*: 1.5 mi N Canaries. *Tobago*: Bucco Bay; Grafton Estate. *Trinidad*: St. George Co., Curepe C.I.B.C. Union. FRENCH WEST INDIES: *Guadeloupe*: Sur Cotonnier. *Martinique*: Diamant; Sainte Anne. BARBADOS: Edge Hill; Freshwater Bay; Groves St. George. CURAÇAO.

*Comments.* *Thyanta testacea* is very closely related to the other species in the *maculata* group, and can be reliably identified only by examination of the male genitalia. The apically acute parameres curving gently dorsad will separate it from all congeners except *T. patruelis*, which it closely resembles. The chin-like protuberance on the posteroventral surface of the pygophore is somewhat less prominent in *T. testacea* than in *T. patruelis*. There does seem to be a geographical separation of the two forms with *T. testacea* restricted to northern South America and the Lesser Antilles, and *T. patruelis* occurring from northeastern Brazil and southern Peru southward.

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versity, Raleigh, C. Parron; NDSF—North Dakota State University, Fargo, E. U. Balsbaugh, Jr.; NMSU—New Mexico State University, Las Cruces, G. S. Forbes, J. R. Zimmerman; ODAS—Oregon Department of Agriculture, Salem, R. L. Westcott; OSU—Ohio State University, Columbus, C. A. Triplehorn; OSUC—Oregon State University, Corvallis, K. A. Phillips; POLH—University of Colorado, Polhemus collection, Englewood, J. T. Polhemus; PUL—Purdue University, West Lafayette, IN, A. V. Provonsha; SIUC—Southern Illinois University, Carbondale, J. E. McPherson; SMEK—Snow Museum of Entomology, University of Kansas, Lawrence, P. D. Ashlock; TAMU—Texas A&M University, College Station, J. C. Schaffner; UAT—University of Arizona, Tucson, F. G. Werner; UCB—Essig Museum of Entomology, University of California, Berkeley, J. A. Powell; UCR—University of California, Riverside, S. I. Frommer; UCS—University of Connecticut, Storrs, J. E. O'Donnell; UGA—University of Georgia, Athens, C. L. Smith; UIM—University of Idaho, Moscow, J. B. Johnson; UMAA—University of Michigan, Ann Arbor, B. M. O'Conner; UMC—University of Missouri, Columbia, R. L. Blinn, T. R. Yonke; UNAM—Instituto de Biología, Universidad Nacional Autónoma de Mexico, Mexico City, DF, H. Brailovsky; UNL—University of Nebraska, Lincoln, B. C. Ratcliffe; USNM—U.S. National Museum of Natural History, Washington, DC, R. C. Froeschner, T. J. Henry; UUSL—University of Utah, Salt Lake City, J. Loye; VPI—Virginia Polytechnic Institute and State University, Blacksburg, M. Kosztarab; WSU—Washington State University, Pullman, R. S. Zack.

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We also thank D. J. Schotzko and F. Merickel, University of Idaho, who generously sent specimens of *T. pallidovirens* preserved in Carnoy's solution for some of the chromosome work discussed in this paper. The chromosome study was also assisted by a Sigma Xi Grant-in-Aid of Research and a Theodore Roosevelt Fund Field Research Grant.

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## REVISION OF *AROCERA* SPINOLA, WITH THE DESCRIPTION OF TWO NEW SPECIES (HETEROPTERA: PENTATOMIDAE)<sup>1</sup>

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**Abstract.**—*Arocera* Spinola contains two subgenera, the nominate subgenus and *Euopta* Stål. Diagnoses are provided for *Arocera*, *Euopta*, and all previously described species. Two new species are described: *A. (Euopta) variegata* from Argentina and *A. (Euopta) sexpunctata* from Ecuador. *Arocera apta* (Walker) and *A. melanopyga* (Stål) are resurrected from the synonymy of *A. spectabilis* (Drury), *A. placens* (Walker) is resurrected from the synonymy of *A. nigrorubra* (Dallas), *A. aequinoxialis* (Westwood) is resurrected from the synonymy of *A. acroleuca* (Perty), and *A. repleta* is resurrected from the synonymy of *A. elongata* and placed as a subspecies of that species. *Arocera affinis* Distant, 1880, *A. protea* Distant, 1880, *A. altivola* Distant, 1893, *A. chiriquensis* Distant, 1893, and *A. contralineata* Pirán, 1955 are all removed from the synonymy of *A. nigrorubra* (Dallas, 1851) and are placed as new synonyms of *A. placens* (Walker, 1867). *Arocera patibulata* Distant, 1880 and *A. jalapensis* Distant, 1893 are both removed from the synonymy of *A. spectabilis* (Drury, 1782) and are also placed as new synonyms of *A. placens*. *Arocera crucigera* Haglund, 1868 and *A. schumanni* Distant, 1890 are both removed from the synonymy of *A. spectabilis*; *A. crucigera* is placed as a new synonym of *A. apta* (Walker, 1867), and *A. schumanni* is placed as a new synonym of *A. melanopyga* (Stål, 1858). Lectotypes are designated for *A. affinis*, *A. schumanni*, *Pentatoma aequinoxialis*, *Strachia apta*, and *S. nigro-rubra*. A key is provided to aid in the identification of species of *Arocera*.

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The genus *Arocera* Spinola *sensu lato* was revised by McDonald in 1984, but the discovery of two undescribed species and several taxonomic problems have necessitated a new revision of the genus. Rider (1991) divided *Arocera* into two genera based primarily on differences in coloration, punctuation, and the male and female genitalia. He transferred seven species of *Arocera* [*colombiana* McDonald, *inmaculata* (Pirán), *principalis* (Stål), *rufolimbata* Stål, *rufonotata* Stål, *splendens* (Blanchard), and *verdana* McDonald] into his newly described genus *Rhysocephala*. He provided diagnoses for all known species and described three new species.

*Arocera* belongs in the nominate tribe and subfamily of the Pentatomidae and is characterized by the lack of a spine or tubercle on the third (second visible) abdominal sternite and by elongate ostiolar rugae, reaching more than half the distance from the ostioles to the lateral metapleural margins. Rolston and McDonald (1984) provided a key to related western hemisphere genera occurring north of South America, and Rolston (1987) provided a key to the South American genera that have both elongate ostiolar rugae and the base of the abdomen unarmed. The species of *Arocera* are some of the most brightly colored species of New World Pentatomidae. Rider (1991) provided a key to the pentatomine genera, which have at least some brightly colored species.

Measurements are in millimeters; measurements in parentheses are of the holotype.

Measurements of the body were taken with the anterior and posterior margins of the scutellum in approximately the same plane of focus. Total length was measured slightly differently between sexes. In females, total length was simply the distance from the apex of the head to the posterior apex of the body excluding hemelytral membranes. Because in males the pygophore may be distended by varying amounts, total length was measured from the apex of the head to the posterior-most part of the last connexival segment. Total width was measured across the humeral angles, although in some cases the width across the abdomen was greater. Head length was measured from the apex of the head to an imaginary line drawn through the posterior margins of the ocelli. Head width was measured across the eyes. When label data are presented in the text, each letter in parentheses represents a separate label with (a) being closest to the specimen. Type label data is cited as written and placed within quotation marks. Determination labels and collection labels were sometimes omitted from the label data citations for brevity. Acronyms are defined in the acknowledgments.

*Arocera* Spinola, 1837

*Arocera* Spinola, 1837:316–318; Stål, 1861:139; Stål, 1867:529; Stål, 1872:37; Distant, 1880:72–73; Lethierry and Severin, 1893:158; Kirkaldy, 1909:109; Froeschner, 1981:68; Rolston and McDonald, 1984:74, 75; McDonald, 1984:97–99; Rolston, 1987:63, fig. 5.

*Ooedosoma* Amyot and Serville, 1843:128 [synonymized by Stål, 1872].

*Estphoria* Gistel, 1848:VIII (replacement name for *Ooedosoma*) [synonymized by Kirkaldy, 1909].

*Type species.* *Arocera*: *Arocera aurantiaca* Spinola, 1837 (=*Pentatoma acroleucum* Perty, 1833), by monotypy. *Ooedosoma*: *Pentatoma acroleucum* Perty, 1833, by monotypy.

*Diagnosis.* Dorsal coloration usually yellow, orange, or red, with black markings (specimens of *A. elongata elongata* are black with orange markings); dorsal punctuation minute, sparse, especially on pronotum.

Vertex and jugal surfaces glabrous with at most a few weak wrinkles on juga; lateral jugal margins slightly reflexed, becoming inflated near apices; juga and tylus subequal in length or juga slightly longer than tylus. First antennal segment reaching nearly to apex of head. Rostrum reaching hind coxae or beyond; first rostral segment reaching slightly beyond posterior terminations of bucculae; bucculae not lobed posteriorly.

Anterolateral pronotal margins reflexed; humeral angles rounded. Ostiolar rugae elongate, curving slightly cephalad, each extending about two-thirds distance from mesial margin of ostiole to lateral metapleural margin. Third (second visible) abdominal segment unarmed. Tarsi three-segmented.

Posteroventral surface of pygophore forming obtuse, semicircular carina; surface of pygophore between carina and inferior ridge lacking black spicules, but often with irregular wrinkles or carinae (Fig. 40); dorsolateral angles of inferior ridge not produced into spiculate horns. Lateral wall of genital cup with large, minutely striated, sclerotized tubercle (Fig. 41, sct); superior ridge prominent, usually expanding over posterolateral angles of proctiger. Each paramere with basal process either obtuse (Fig. 29, tub) or large and spatulate (Fig. 49, bsp). Posterior margin of proctiger entire,

not produced caudally (Fig. 13). Ninth paratergites flat to slightly concave (Fig. 19). Spermathecal bulb either constricted near base (Fig. 4) or armed with long digitiform process (Fig. 6), not simply globose; dilation of spermatheca entirely membranous, lacking slightly sclerotized area proximally (Fig. 1).

*Comments.* Stål (1872) divided the genus *Arocera* into two subgenera based primarily on the shape of the head and the length of the first antennal segment. He included only one species, *A. acroleuca*, in the nominate subgenus, but he considered *A. acroleuca* and *A. aequinoxialis* to be synonyms. They are both valid species and can be separated from the remaining species by the distinctive dorsal coloration, the shape of the head, and the form of the female genital plates. The remaining eight species known to Stål were placed in the subgenus *Euopta* Stål, but three of these, *A. rufolimbata*, *A. rufonotata*, and *A. splendens*, Rider (1991) transferred to the genus *Rhysscephala*. McDonald (1984) described *A. colombiana* and *A. verdana*, both of which were also transferred to *Rhysscephala*. Pirán (1963) described *Pharypia inmaculata* which Grazia (1986) transferred to *Arocera*. Rider (1991) then transferred *A. inmaculata* to *Rhysscephala*. Three valid species and one subspecies have been added to *Arocera* since the work of Stål. Walker (1867) described *Strachia apta* and *S. placens* which were both later transferred to *Arocera*. Showalter (1929) inadvertently "described" *A. elongata* when he published a picture of the species with a manuscript name of Uhler's in an issue of National Geographic. In 1929, this was sufficient for a valid species description. Finally, Van Duzee (1931) described *A. repleta* which is here considered a subspecies of *A. elongata*.

One species has been placed in *Arocera* and was subsequently transferred to another genus. Walker (1867) described *Strachia nigropicta* from at least two specimens from Brazil. Distant (1900) transferred this species to *Arocera*. Later, Rolston (1976) transferred it to the genus *Pharypia*, placing it as a junior synonym of *P. generosa* Stål. Rolston also made lectotype and paralectotype designations.

At present eleven species and one subspecies are recognized in *Arocera*.

#### KEY TO THE SUBGENERA AND SPECIES OF *AROCERA* SPINOLA

1. Dorsal surface pale yellow with large, U-shaped black marking (Figs. 25, 32); dorsal surface of head transversely concave; ninth paratergites slender, width less than half the length (Fig. 21) subgenus *Arocera* Spinola ..... 2
- Dorsal surface yellow, orange, or red with dark brown or black macules, but not forming U-shaped marking; dorsal surface of head flat to slightly concave; ninth paratergites relatively broad, width greater than half the length (Figs. 19, 20) subgenus *Euopta* Stål ..... 3
- 2(1). Femora fuscous to black except, at most basal one-fourth yellow with margin between yellow and black areas gradual, diffuse; lateral margins of black, U-shaped marking on dorsum usually entire, extending laterad over distal end of R + M vein (Fig. 25) (southern and eastern South America) ..... *acroleuca* (Perty)
- Femora fuscous to black on distal one-half, basal one-half yellow with margin between yellow and black areas sharp, well-defined; lateral margins of black, U-shaped, dorsal marking usually emarginate near apex of corium, usually not extending laterad over distal end of R + M vein (Fig. 32) (northern and western South America) ..... *aequinoxialis* (Westwood)

- 3(1). Antennal segment I fuscous or black, concolorous with rest of antennal segments ..... 4
- Antennal segment I yellow, orange, or red, distinctly lighter in color than rest of antennal segments ..... 6
- 4(3). Posterolateral angles of pygophore armed with 1–3 minute, medially directed teeth (Fig. 40); each paramere in ectal view uniformly elongate, apex curving only slightly laterad (Fig. 43) (Colombia) ..... *nigrorubra* (Dallas)
- Posterolateral angles of pygophore unarmed (Figs. 46, 55); each paramere in ectal view sinuously elongate, apex curving distinctly laterad (Figs. 51, 60) ..... 5
- 5(4). Posteroventral surface of pygophore with relatively deep, semicircular depression and sharply carinate ventral margin; in ectal view, lateral margin of each paramere distinctly sinuous, subapical notch well-defined (Fig. 50), (Bolivia and northern Argentina) ..... *variegata* new species
- Posteroventral surface of pygophore with relatively shallow, semicircular depression, and obtusely carinate ventral margin; in ectal view, lateral margin of each paramere slightly sinuous, subapical notch not distinct (Fig. 59) (Mexico and Jamaica south to Argentina) ..... *placens* (Walker)
- 6(3). Rostrum reaching onto posterior half of fifth (fourth visible) abdominal segment, often reaching onto sixth abdominal segment; dorsal surface bright orange with hemelytral membranes and ocellar areas of head black (Figs. 61, 69), or black with most of head, apex of scutellum, and two spots on each corium orange (Fig. 62) ..... 7
- Rostrum at most reaching on to anterior half of fifth (fourth visible) abdominal segment; dorsal surface yellow or orange with brown or black macules ..... 9
- 7(6). Dorsal surface mostly black with six orange spots, one on head, one on basal third of each corium, one on posterolateral angle of each corium, and one on apex of scutellum (Fig. 62), spot on apex of scutellum sometimes continued cephalad as thin orange line (northwestern South America) ..... *elongata elongata* Showalter
- Dorsal surface mostly orange, sometimes with a few small black markings ..... 8
- 8(7). Dorsal surface usually completely orange except for black hemelytral membranes and black spot around each ocellus (Fig. 61), sometimes with other black macules, but never in pattern described below; each paramere in ectal view not curving laterad apically (Fig. 68) (Panama and Costa Rica) ..... *elongata repleta* Van Duzee
- Dorsal surface orange except for base of head, hemelytral membranes and six small spots black: one on each basal angle of scutellum, one on each side of midline of scutellum about one-half distance from base to apex, and one on each side of midline of pronotum (Fig. 69); each paramere in ectal view curving distinctly laterad apically (Fig. 75) (Ecuador) ..... *sexpunctata* new species
- 9(6). Ocelli very small, distance from each ocellus to adjacent eye at least 3–4 times diameter of ocellus; dorsal margin of each paramere in lateral and medial views concave (Figs. 80, 81) (northwestern South America) ..... *ruffrons* (Dallas)
- Ocelli of normal size, distance from each ocellus to adjacent eye no more than 1–2 times diameter of ocellus; dorsal margin of each paramere in lateral and medial views distinctly sinuous (Figs. 87, 88, 94, 95, 101, 102) ..... 10
- 10(9). In lateral and medial views dorsal margin of each paramere with basal emargination very shallow (Figs. 87, 88) (Mexico and northern Central America) ..... *melanopyga* (Stål)
- In lateral and medial views, dorsal margin of each paramere with basal emargination relatively deep (Figs. 94, 95, 101, 102) (Costa Rica, Panama, and South America) ..... 11
- 11(10). Humeral angles black (Fig. 90); connexiva alternately fuscous and pale yellow

- (Fig. 90); usually with black spots on abdominal venter (southern and eastern Brazil) ..... *spectabilis* (Drury)
- Humeral angles yellow (Fig. 97); connexiva uniformly pale yellow (Fig. 97); abdominal venter uniformly pale yellow except for some black markings on basal plates (northern and western South America) ..... *apta* (Walker)

### Subgenus *Arocera* Spinola, 1837

**Diagnosis.** Dorsal coloration pale yellow with large, U-shaped, black marking, open end on base of pronotum, closed end on hemelytral membranes (Figs. 25, 32). Dorsal surface of head distinctly, transversely concave. Posterolateral angles of pygophore prominent in lateral view, apices ventral to middle of pygophore (Figs. 28, 35). Each paramere with obtuse basal process, lacking large spatulate process (Figs. 29, 36). Ninth paratergites elongate, slender, width less than half the length (Fig. 21); spiracles on eighth paratergites exposed, clearly visible. Spermatheca with sclerotized rod swollen near proximal ends (Figs. 1, 3), spermathecal bulb constricted near base, with or without digitiform process (Figs. 2, 4).

**Comments.** The difference between *Arocera* and *Euopta* are distinct and involve both the male and female genitalia, and the two subgenera could be elevated to genera. They do, however, have a number of characters in common, and so I have chosen to recognize them as subgenera. The subgenus *Arocera* contains only two very closely related species, *A. acroleuca* and *A. aequinoxialis*.

#### *Arocera (Arocera) acroleuca* (Perty, 1833)

Figs. 1, 2, 25–31, Map 1

*Pentatoma acroleucum* Perty, 1833:168, pl. 33, fig. 11.

*Cimex acroleucus*: Burmeister, 1835:366.

*Arocera aurantiaca* Spinola, 1837:318; Herrich-Schäffer, 1844:90 [synonymized by Signoret, 1851].

*Oedosoma acroleucum*: Amyot and Serville, 1843:128.

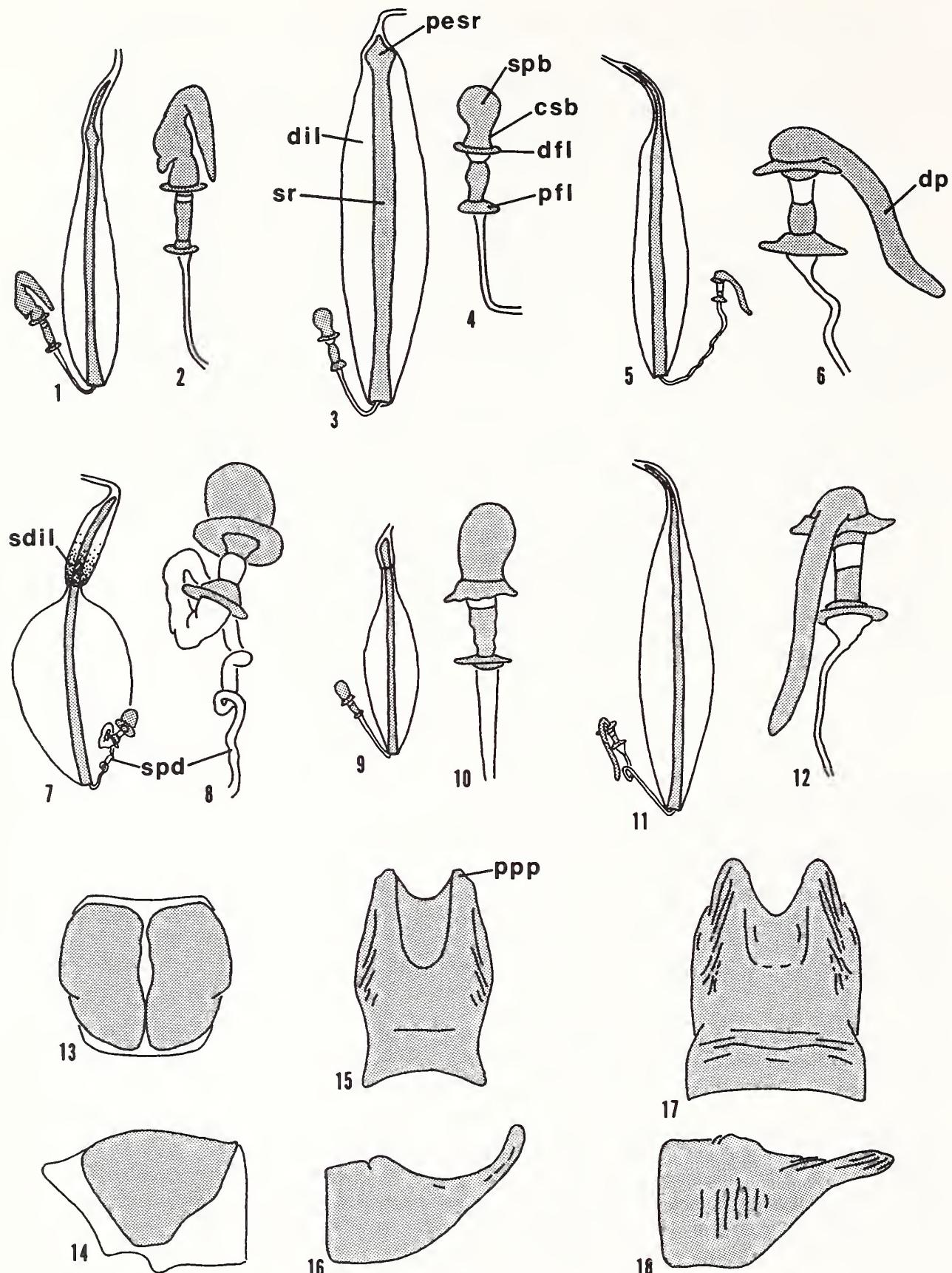
*Strachia acroleuca*: Dallas, 1851:263; Signoret, 1851:338; Stål, 1860:22; Walker, 1867:318.

*Arocera acroleuca*: Stål, 1861:140; Distant, 1880:73 (part); Lethierry and Severin, 1893:158–159 (part); Pirán, 1966:86; McDonald, 1984:102–103, figs. 9–16 (part).

*Arocera (Arocera) acroleuca*: Stål, 1872:38 (part); Kirkaldy, 1909:109 (part).

**Diagnosis.** Dorsal surface yellow with large, U-shaped, black marking; lateral margins of U-shaped mark usually entire and extending laterad across distal end of R + M vein (Fig. 25). Dorsal surface of head black with a few transverse wrinkles; antennae black. Anterolateral pronotal margins slightly convex (Fig. 25), slightly reflexed. Ventral surface yellow except most of head black; rostrum usually extending onto third (second visible) abdominal segment, yellow except segment IV black. Legs fuscous to black except coxae and trochanters yellow, each femur gradually becoming yellow near base. Extreme distal apices of juga often pale brown, this color sometimes continuing along reflexion of juga.

Posterolateral angles of pygophore continuing onto pygophoral surface as weak, obtuse, semicircular carina; inferior ridge in caudal view distinctly sinuous (Fig. 27). Each paramere in lateral and medial views F-shaped, with small, obtuse protuberance



Figs. 1–18. 1, 2. *Arocera (A) acroleuca*. 1. Spermatheca. 2. Spermathecal pump. 3, 4. *A. (A.) aequinoxialis*. 3. Spermatheca. 4. Spermathecal pump. 5, 6. *A. (Euopta) sexpunctata*. 5. Spermatheca. 6. Spermathecal pump. 7, 8. *Rhysscephala splendens*. 7. Spermatheca. 8. Spermathecal pump. 9, 10. *R. infuscata*. 9. Spermatheca. 10. Spermathecal pump. 11–14. *A. (E.) spectabilis*. 11. Spermatheca. 12. Spermathecal pump. 13. Proctiger, dorsal view. 14. Proctiger, lateral view. 15, 16. *R. macdonaldi*. 15. Proctiger, dorsal view. 16. Proctiger, lateral view. 17, 18. *R. ecuadoriensis*. 17. Proctiger, dorsal view. 18. Proctiger, lateral view. Symbols: csb,

on shaft (Figs. 29, 30); in ectal view paramere-head slightly produced both medially and laterally, distal margin nearly straight (Fig. 31). Sclerotized rod of spermatheca swollen and then somewhat elongate proximally (Fig. 1); spermathecal bulb constricted near base, with one long digitiform process connecting to top of bulb, and one short digitiform process connecting to side of bulb just above constriction (Fig. 2).

**Types.** Perty (1833) described this species from a single ♂ specimen. The type specimen of *Pentatoma acroleuca*, which is housed in the Zoologische Museum, Munich, was examined. The label data for the holotype specimen is (a) "Type. Perty." (b) "Brasilia a: acroleuca Pert" (c) "AROCERA ACROLEUCA Perty".

Spinola (1837) described *Arocera aurantiaca* from Brazil. The type specimen is not in the Spinola collection and was not located, but the description matches either *A. acroleuca* or *A. aequinoctialis* very closely. The type locality of Brazil puts it within the known range of *A. acroleuca*.

**Specimens examined.** 45 specimens collected from 2 October to 9 April; deposited in AMNH, BMNH, DAR, MACN, USNM, ZMB, ZSM. BOLIVIA: Santa Cruz: Tchito, Buena Vista. BRAZIL: Bahia: Encruzilhada; Nova Conquista. Goiás: Anápolis; Chapada dos Veadeiros, 18–24 km N Alta Paraiso; Jataí. Mato Grosso: Campo Grande; Nivac. Minas Geraes: Barroso; Diamantina; Faz. dos Campos; Pedra Azul; Sete Lagoas; Viçosa. Rio de Janeiro: Rio de Janeiro. São Paulo: Campinas; Cipó; São Paulo.

**Distribution.** Eastern and central South America (Map 1).

**Comments.** This species is nearly identical in coloration with *A. aequinoctialis*, and the two were considered conspecific until now. There are distinct differences in both the male and female genitalia as well as a couple of fairly consistent somatic characters. *Arocera acroleuca* has the femora fuscous to black except for at most the basal one-fourth yellow, and the transition from fuscous to yellow is gradual. *Arocera aequinoctialis* has the basal one-half of the femora yellow and the transition from fuscous to yellow is sharp. Both of these species are almost identical in coloration to *Pharypia gracilirostris* Stål but may be separated from that species by the unarmed abdominal venter and the shorter first rostral segment.

#### *Arocera (Arocera) aequinoctialis* (Westwood, 1837)

Figs. 3, 4, 21, 32–38, Map 1

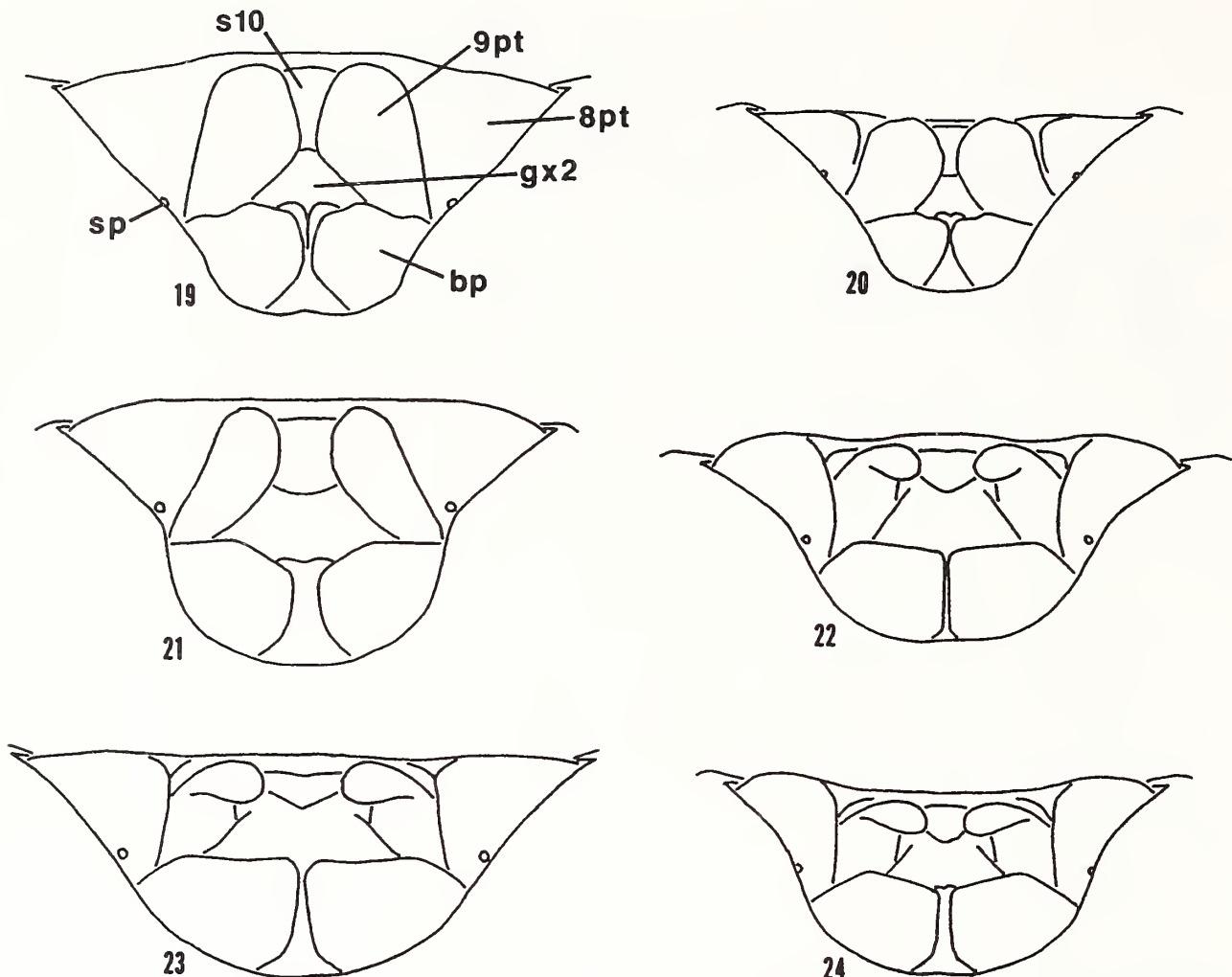
*Pentatoma aequinoctialis* Westwood, 1837:33.

*Arocera acroleuca* (of authors, not Perty): Distant, 1880:73 (part); Lethierry and Severin, 1893:158–159 (part); McDonald, 1984:102–103, figs. 9–16 (part).

*Arocera (Arocera) acroleuca* (of authors, not Perty): Stål, 1872:38 (part); Kirkaldy, 1909:109 (part).



constriction of spermathecal bulb; dfl, distal flange; dil, dilation of spermatheca; dp, digitiform process; pesr, proximal end of sclerotized rod; pfl, proximal flange; ppp, posterior projection of proctiger; sdil, sclerotized portion of dilation of spermathecal duct; spd, spermathecal duct; sr, sclerotized rod; spb, spermathecal bulb.

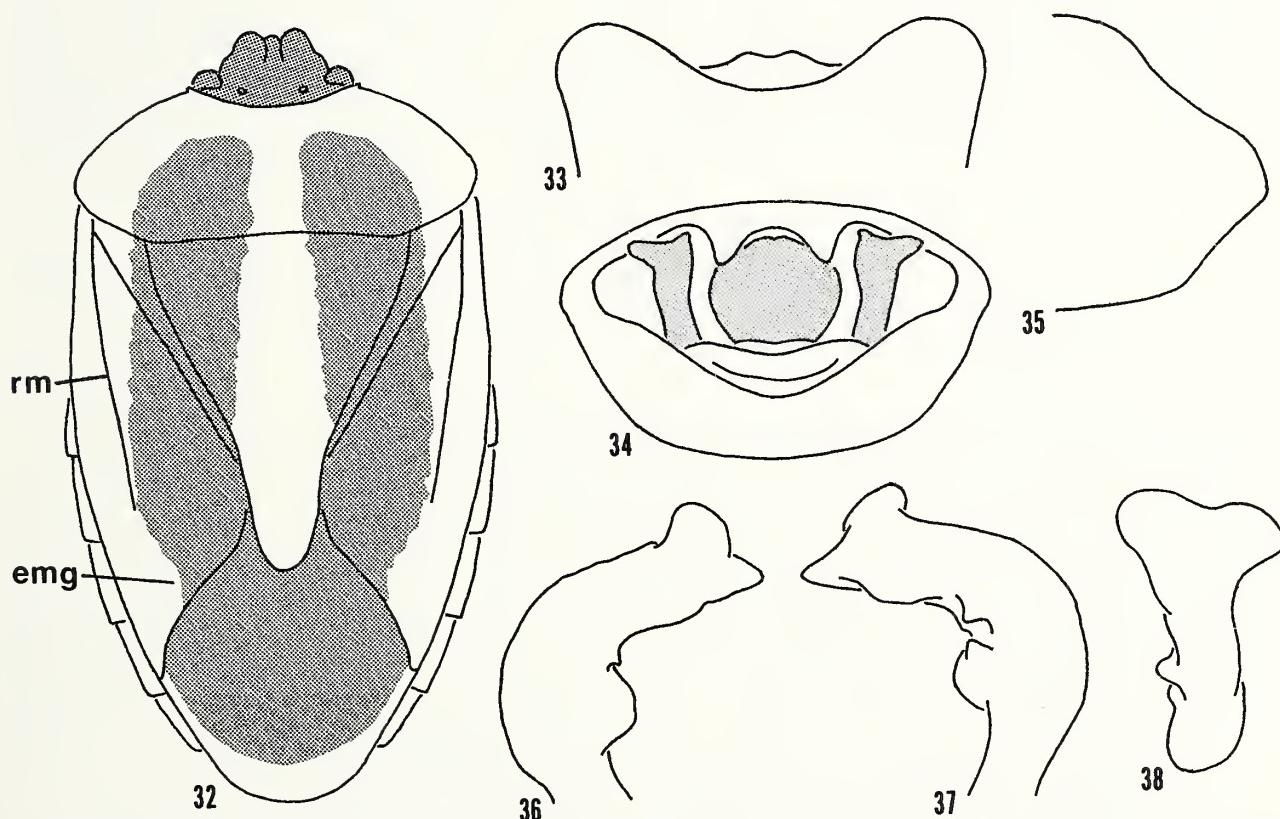
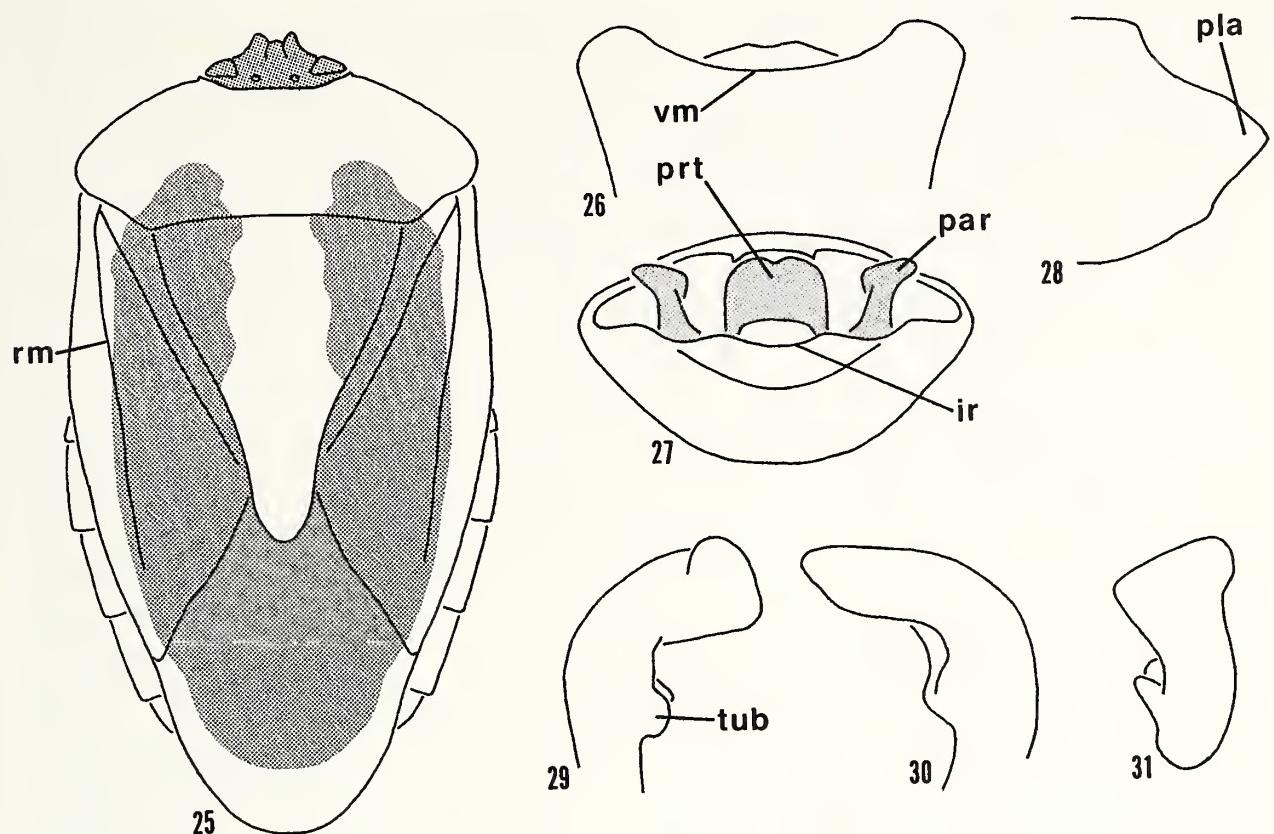


Figs. 19–24. Genital plates. 19. *Arocera (Euopta) sexpunctata*. 20. *A. (E.) variegata*. 21. *A. (A.) aequinoctialis*. 22. *Rhyssoccephala macdonaldi*. 23. *R. ecuadorensis*. 24. *R. infuscata*. Symbols: bp, basal plate; gx2, gonacoxae 2; sp, spiracle; s10, sternite 10; 8pt, eighth paratergite; 9 pt, ninth paratergite.

**Diagnosis.** Coloration essentially the same as *A. acroleuca* except for the following differences: basal half of femora yellow, transition from fuscous to yellow sharp; lateral margins of dorsal, U-shaped, black mark usually indented medially just anterior to hemelytral membranes, black extending laterally sometimes to distal end of each R + M vein, but usually not extending across R + M vein (Fig. 32); apices and reflexion of juga always black.

Posterolateral angles of pygophore continuing onto pygophoral surface as weak, obtuse, semicircular carina; inferior ridge in caudal view distinctly sinuous medially (Fig. 34). Each paramere in lateral and medial views F-shaped, with obtuse protuberance on shaft (Figs. 36, 37); in ectal view paramere-head distinctly produced both medially and laterally, apical margin distinctly concave (Fig. 38). Spermatheca with apex of sclerotized rod swollen, but not elongate proximally (Fig. 3); spermathecal bulb globose with basal constriction, lacking digitiform processes (Fig. 4).

**Types.** Westwood (1837) described *Pentatoma aequinoctialis* without designating a holotype or paratypes. One ♂ syntype and 1 ♀ syntype were located. The ♂ specimen labeled (a) "TYPE. = =WESTW. (HOPE) C. Hemipt. 1837 Part I, page 33 Distant, P. Z. S., 1900, p. 807-825." (b) "Type" (c) "America aq." (d) "aquinoctialis Hope"



Figs. 25–38. 25–31. *Arocera (A.) acroleuca*. 25. Habitus. 26–28. Pygophore. 26. Ventral view. 27. Caudal view. 28. Lateral view. 29–31. Right paramere. 29. Lateral view. 30. Medial view. 31. Ectal view. 32–38. *A. (A.) aequinoxialis*. 32. Habitus. 33–35. Pygophore. 33. Ventral view. 34. Caudal view. 35. Lateral view. 36–38. Right paramere. 36. Lateral view. 37. Medial view. 38. Ectal view. Symbols: emg, lateral emargination in dorsal U-shaped marking; ir, inferior ridge; par, paramere; pla, posterolateral angle of pygophore; prt, proctiger; rm, R + M vein; tub, tubercle near base of paramere; vm, ventral margin of pygophore.



Map 1. *Arocera (A.) acroleuca* (●); *A. (A.) aequinoctialis* (○).

(e) "Pentat. marginalis H Sch: Hahn. 320" (f) "Arocera acroleuca Perty" (g) "TYPE HEM: 167 ½ PENTATOMA AEQUINOXIALIS WESTWOOD HOPE DEPT. OXFORD" is designated the lectotype. The ♀ specimen labeled (a) "Rio" (b) same as (g) for lectotype, is designated paralectotype. Both specimens were examined and are housed in the Oxford Entomological Museum, England.

*Specimens examined.* 86 specimens collected during every month of the year except February; deposited in AMNH, BMNH, CAS, DAR, DBT, HCO, LHR, MACN, USNM, ZMB. GUATEMALA: Morales. COSTA RICA: Guanacaste: Guanacaste. PANAMA: Darién: Santa Fe. COLOMBIA: Amazonas: Leticia. Antioquia: Valley of Medellín. Cauca: Cauca Valle. GUYANA: East Demerara-West Coast Berbice: Rockstone, Essequebok R. SURINAM: Marowijne: Nassau Mts, Marowijne R. FRENCH GUIANA: Cayenne: Cayenne; Crique Boulanger; Hwy D6 to Kaw, 33.5 km SE Roura; Hwy N2 to Regina, 67 km S Cayenne. ECUADOR: Pastaza: Cuisimi, on Rio Cuisimi, 150 km SE Puyo. PERU: Archinamiza. Cusco: Quince Mil. Huanuco: Tingo María, Rio Huallaga. Loreto: Iquitos, Amazon R; Rio Tapiche; middle Rio Ucayali. Madre de Dios: Rio Tabopata Reserve, 30 km SW Puerto Maldonado. San Martín: El Boquerón Pass; Palmas del Espino Uchiza. BOLIVIA: Las Juntas; Sara. El Beni: Reyes. La Paz: Tumupasa. Santa Cruz: Buena Vista; Saavedra Expt. Stn.; Santa Cruz. BRAZIL: Amazonas: Tefé. Mato Grosso: Corumba Pará: Santarém.

*Distribution.* Central America and northern and western South America (Map 1).

*Comments.* This species is very closely related to *A. acroleuca* but may be separated from that species by differences in both the male and female genitalia and usually by several color characters. The basal half of each femur is yellow, and the boundary between the fuscous and yellow areas is sharp; the same boundary in *A. acroleuca* is gradual, and only the basal one-fourth of the femur is yellow.

#### Subgenus *Euopta* Stål, 1872

*Arocera (Euopta)* Stål, 1872:38; Kirkaldy, 1909:109.

*Type species.* *Cimex spectabilis* Drury, 1782, by subsequent designation (Kirkaldy, 1909:XXX).

*Diagnosis.* Dorsal coloration yellow, orange, or red, with black markings, but not forming distinct U-shaped marking. Dorsal surface of head flat to only slightly concave. Pygophore with posterolateral angles prominent in lateral view, apices dorsal to middle of pygophore (Fig. 42). Each paramere C-shaped, with large, spatulate process near base (Fig. 49). Ninth paratergites relatively broad, width greater than half length (Figs. 19, 20); spiracles on eighth paratergites small, entirely or partially concealed under seventh abdominal tergites. Sclerotized rod of spermatheca acuminate and curved proximally, not swollen (Figs. 5, 11); spermathecal bulb not constricted basally, possessing single, long, digitiform process (Figs. 6, 12).

*Comments.* The above characters will easily separate the species of this subgenus from the species of the nominate subgenus.

The species of this subgenus may be grouped into three species groups. *Arocera elongata* and *A. sexpunctata*, the largest species, have the first antennal segment pale, the hemelytral membranes completely black, and the parameres similarly shaped. *Arocera nigrorubra*, *A. placens*, and *A. variegata*, the smallest species, have the first antennal segment black, the hemelytral membranes black with the posterior margins

pale, and the paramere-head and basal, spatulate process nearly parallel. *Arocera apta*, *A. melanopyga*, *A. rufifrons*, and *A. spectabilis* are medium-sized and have the first antennal segment pale, the hemelytral membranes black with the posterior margins pale, and the paramere-head and basal spatulate process nearly perpendicular.

*Arocera (Euopta) nigrorubra* (Dallas, 1851)  
Figs. 39–43, Map 2

*Strachia nigrorubra* Dallas, 1851:267; Walker, 1867:318.

*Strachia quadripunctata* Signoret, 1851:337, pl. 10, fig. 4 [synonymized by Stål, 1872].

*Arocera nigrorubra*: Stål, 1861:140; Lethierry and Severin, 1893:159; Rolston, 1976: 3; McDonald, 1984:105–108, figs. 26–36 (part).

*Arocera (Euopta) nigrorubra*: Stål, 1872:38; Kirkaldy, 1909:109.

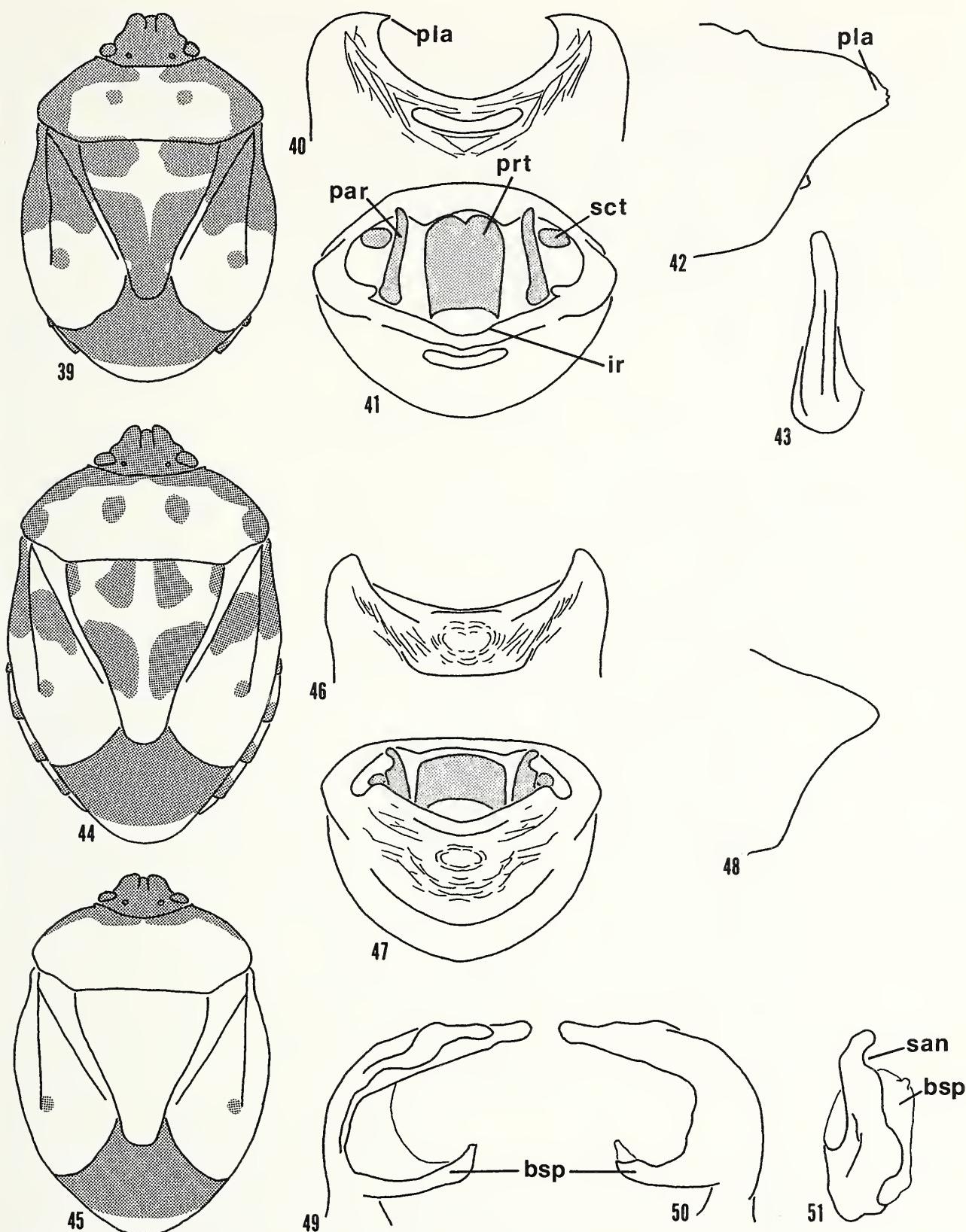
**Diagnosis.** Dorsal surface of head entirely black, with weak, transverse striations on bases of juga; apex of head rounded. Lateral jugal margins reflexed, sinuous; apices of juga somewhat inflated. Antennal segment I black (remainder of antennae missing in only known specimen). Dorsal surface of pronotum orange-red with anterior (except medially) and anterolateral margins and humeral angles black; and with small, black spot on each side of middle (Fig. 39). Scutellum black with orange-red, cruciform marking, posterior part of cross not reaching apex of scutellum; small, orange-red spot laterally on each side near inner corial angle. Basal one-third to one-half of each corium black except orange intruding anteriorly for short distance on clavus; small, round, black spot just mesial to apex of each R + M vein; embolium much wider apically than basally; posterior margins of coria convex (Fig. 39). Hemelytral membranes black with posterior margins pale (Fig. 39). Connexiva alternately black and orange-red.

Ventral surface of head and thorax completely black; rostrum black, extending to base of abdomen; legs black. Abdominal sternites orange-red laterally, black medially, except last segment orange-red with medial, chordate, black spot; posterolateral angles black, and small, black spot surrounding each spiracle.

Posteroventral surface of pygophore with semicircular impression, and weak submarginal carina parallel to posterior margin of pygophore becoming prominent medially; posterior margin in ventral view arcuately rounded, posterolateral angles armed with two to three minute, medially-directed teeth (Fig. 40). Parameres uniformly elongate, each lacking subapical emargination, narrowly rounded apically in ectal view, curving only slightly laterad (Fig. 43). Female unknown.

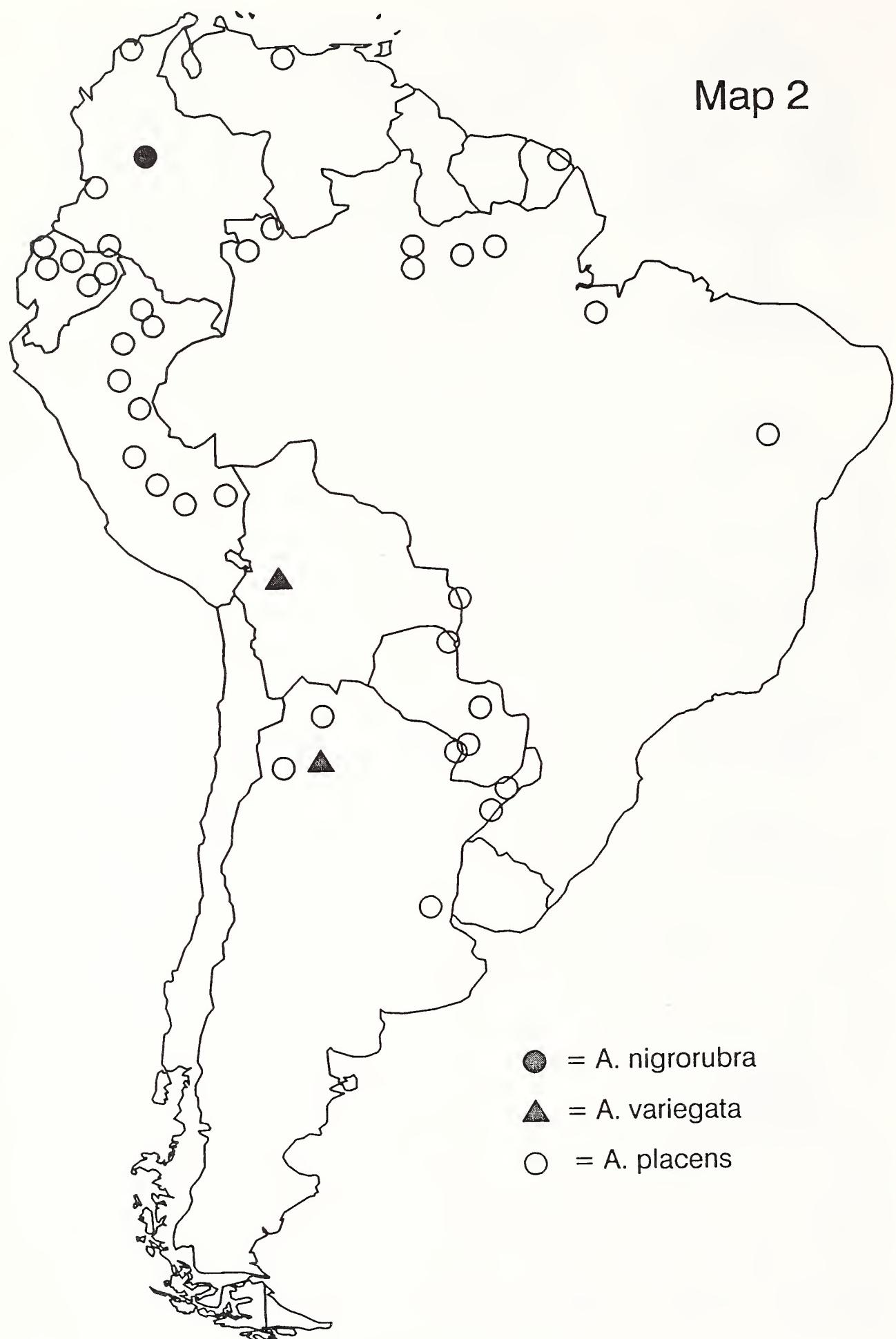
**Types.** Dallas (1851) described *Strachia nigrorubra* from an indeterminate number of specimens from Colombia without designating a holotype or paratypes. Only one syntype specimen, a ♂, was located and is here designated lectotype. It has the following label data: (a) "Type" (b) "Colombia" (c) "fusagasuga Rolu." (d) "33. STRACHIA NIGRORUBRA." This specimen was examined and is conserved in the British Museum (Natural History), London.

The type specimen of *Strachia quadripunctata* Signoret, 1851 was not examined, but the figure in the original description is of a specimen with a nearly identical color pattern as that of the holotype of *S. nigrorubra*. Until further evidence is discovered, it seems best to leave this species as a junior synonym of *A. nigrorubra*.



Figs. 39–51. 39–43. *Arocera (Euopta) nigrorubra*. 39. Habitus. 40–42. Pygophore. 40. Ventral view. 41. Caudal view. 42. Lateral view. 43. Left paramere, ectal view. 44–51. *A. (E.) variegata*. 44, 45. Habitus. 46–48. Pygophore. 46. Ventral view. 47. Caudal view. 48. Lateral view. 49–51. Right paramere. 49. Lateral view. 50. Medial view. 51. Ectal view. Symbols: bsp, basal spatulate process; ir, inferior ridge; par, paramere; pla, posterolateral angle of pygophore; prt, proctiger; san subapical notch; sct, sclerotized tubercle.

Map 2

Map 2. *Arocera (Euopta) nigrorubra* (●); *A. (E.) placens* (○); *A. (E.) variegata* (▲).

*Distribution.* Colombia (Map 2).

*Specimens examined.* This species is known only from the type specimen.

*Comments.* Although the only known specimen is distinctively marked, the markings are not unique. I have examined several specimens of *A. placens* with very similar markings. The only reliable method to separate these two species and also the closely related *A. variegata* is by the male genitalia. In both *A. placens* and *A. variegata*, the lateral surface of each paramere in ectal view is distinctly sinuous with the apex curving distinctly laterad. Each paramere of *A. nigrorubra* is more uniform in shape with the apex curving only slightly laterad. Also, the two to three medially directed teeth on each posterolateral angle of the pygophore of *A. nigrorubra* are diagnostic.

***Arocera (Euopta) variegata*, new species**

Figs. 20, 44–51, Map 2

*Description.* Broadly oval, somewhat convex above, distinctly convex below; dorsal coloration variable, but usually yellow to orange with black markings; dorsal punctuation very weak, indistinct, especially on pronotum and basal disc of scutellum.

Dorsal surface of head black, usually with apices of juga becoming brown; jugal surfaces weakly wrinkled; lateral jugal margins sinuous, nearly parallel, narrowly but distinctly reflexed, becoming slightly inflated distally; juga slightly longer than tylus. Antennae entirely fuscous to black. Ocelli relatively small, distance from each ocellus to adjacent eye at least one and one-half times diameter of ocellus.

Anterolateral pronotal margins slightly convex, distinctly reflexed; pronotal disc yellow to orange with anterior margin and sometimes anterolateral margins black, often forming black spot on each humeral angle, and on each side of midline of pronotal disc (Fig. 44). Scutellum usually yellow or orange with six black macules: a small spot in each basal angle, two larger spots medially along base, one large, subtriangular spot near distal end of each frenum (Fig. 44), and sometimes one small spot on apex; sometimes scutellum entirely pale, lacking black markings (Fig. 45). Coria yellow to orange with basal one-fourth to one-third black, sometimes with pale coloration continuing cephalad on each clavus and onto basal portions of each corium (Fig. 44); each corium with small black spot near distal end of R + M vein, sometimes lacking black markings except for this spot (Fig. 45); hemelytral membranes fumose with margins transparent. Connexiva yellow or orange with posterior one-third of each segment fuscous to black (Fig. 45).

Ventral surface of head and thoracic segments fuscous to black. Rostrum fuscous to black, extending onto base of abdomen. Legs entirely fuscous to black, except sometimes coxae brown. Ventral surface of abdomen yellow to orange with transverse black spots medially, those near base widest and becoming gradually narrower on distal segments, there forming triangular black area medially; also with black spot in each posterolateral angle of abdominal sternites and black spot just mesad and cephalad of each spiracle; spiracle usually just in edge of black spot.

Posterior margin of pygophore in ventral view concave, posterolateral angles unarmed (Fig. 46); weak submarginal carina parallel to posterior margin becoming wrinkled tumescence medially (Figs. 46, 47); posteroventral surface with relatively deep, semicircular depression; ventral margin sharply carinate (Fig. 47). Each par-

amere C-shaped, distal part sinuously elongate in ectal view with relatively deep subapical notch, apex curving distinctly laterad (Fig. 51); basal, spatulate process projecting in approximately same plane as paramere-head. Basal plates widely separated basally, converging distally, mesial margins somewhat convex, posteromesial angles rounded, posterior margins slightly sinuous mesially (Fig. 20).

**Measurements.** Total length 9.78–11.83 (9.78); total width 5.99–7.10 (5.99); medial length of pronotum 2.05–2.37 (2.05). Medial length of scutellum 4.31–5.19 (4.31); basal width 4.36–4.53 (4.36); width at distal end of frena 1.66–2.21 (1.66). Length of head 1.71–1.93 (1.71); width 2.51–2.84 (2.51); intraocular width 1.44–1.60 (1.44); intraocellar width 0.85–0.98 (0.85); ocellar diameter 0.15; distance from ocellus to adjacent eye 0.24–0.29 (0.26). Length of segments I–V of antennae 0.40–0.55 (0.55), 0.85–1.07 (0.85), 1.18–1.25 (1.21), 1.56–1.64 (1.56), and 1.69–1.71 (1.71), respectively. Length of segments II–IV of rostrum 1.44–1.62 (1.44), 1.14–1.36 (1.14), and 1.03–1.12 (1.07), respectively.

**Holotype.** ♂ labeled "ARGENTINA, Horca Molle, near Tucuman X-18-1968 C.W. & L.B. O'Brien." Deposited in the Florida State Collection of Arthropods, Gainesville.

**Paratypes.** 3 ♀ specimens. (a) "ARGENTINA: Prov. Tucumán, Acheral, 350 m, 9.XII.1966 leg. W. Weyrauch" (b) "ex-col Weyrauch" (♀ LHR); "S. P. Cololao Tucumán 1950 Leg. J. M. Arnau" (♀ MACN); "SUR-YUNGAS CHULUMANI-1-48 BRIDAROLLI" [location in Bolivia] (♀ MACN).

**Distribution.** Bolivia and northern Argentina (Map 2).

**Comments.** This species is most closely related to *A. nigrorubra* and *A. placens*, and may be reliably separated from those species only by the male genitalia. In *A. nigrorubra* each paramere in ectal view is uniformly elongate with the apex curving only slightly laterad, and the posterolateral angles of the pygophore are armed with several small teeth. In both *A. placens* and *A. variegata* each paramere in ectal view is sinuously elongate with the apex curving distinctly laterad, and the posterolateral angles of the pygophore are unarmed. *Arocera placens* has the ventral margin of the pygophore obtusely carinate, whereas *A. variegata* has the ventral margin of the pygophore sharply carinate.

**Etymology.** This species is named *variegata* to reflect its variable coloration.

#### *Arocera (Euopta) placens* (Walker, 1867)

Figs. 52–60, Maps 2, 4

*Strachia placens* Walker, 1867:316–317.

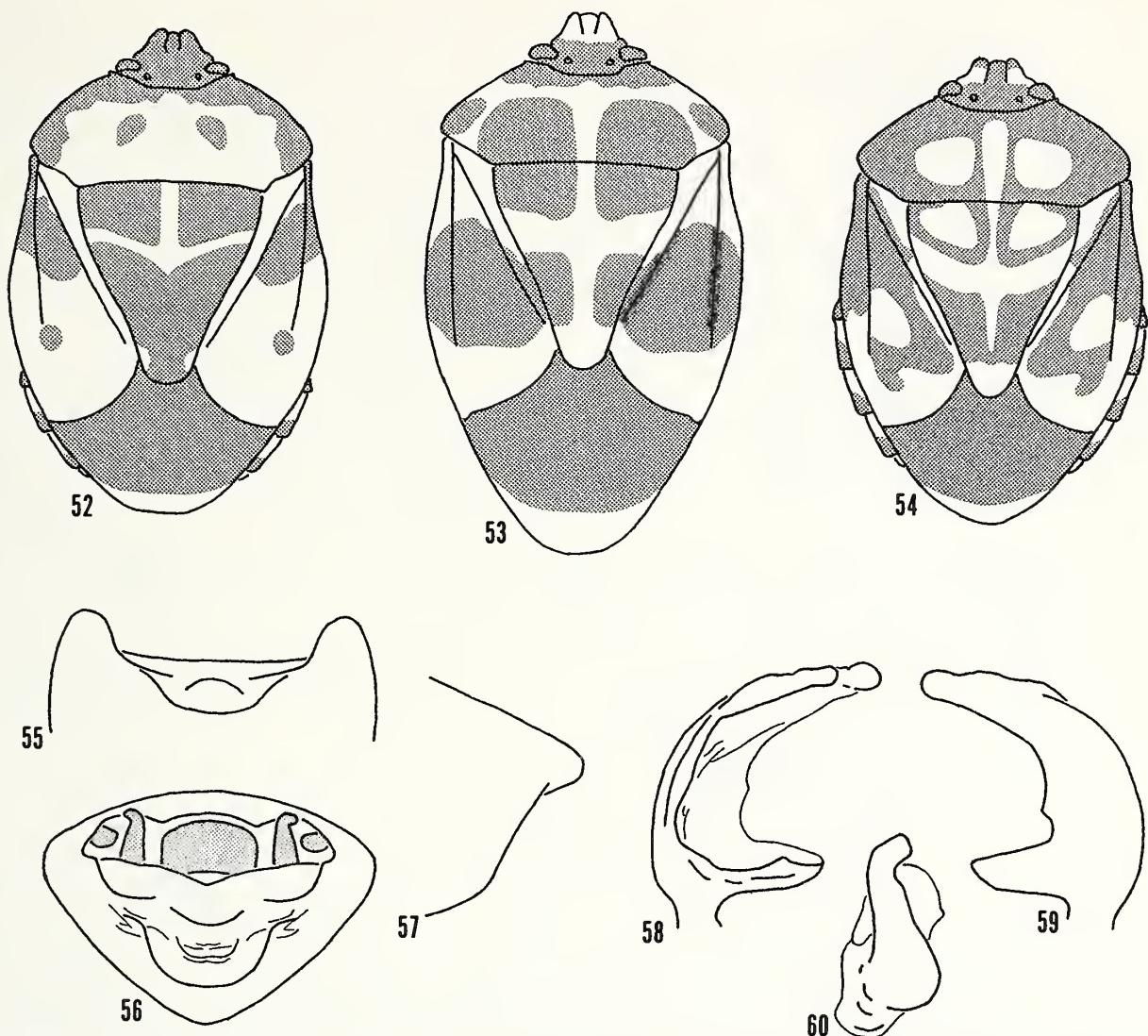
*Arocera protea* Distant, 1880:73–74, pl. 7, fig. 18; Distant, 1893:336; Lethierry and Severin, 1893:159; Rolston, 1976:3; Froeschner, 1981:68; Brailovsky and Barrera, 1982:237. **NEW SYNONYMY.**

*Arocera affinis* Distant, 1880:74, pl. 7, fig. 19; Distant, 1893:336; Lethierry and Severin, 1893:159; Rolston, 1976:3; Brailovsky and Barrera, 1982:236–237. **NEW SYNONYMY.**

*Arocera patibulata* Distant, 1880:74, pl. 7, fig. 17. **NEW SYNONYMY.**

*Arocera altivola* Distant, 1893:337, pl. 31, fig. 18; Lethierry and Severin, 1893:159; Rolston, 1976:3. **NEW SYNONYMY.**

*Arocera chiriquensis* Distant, 1893:337, pl. 30, fig. 19; Lethierry and Severin, 1893:159; Becker and Grazia-Vieira, 1971:11; Rolston, 1976:3; Grazia, 1984:73. **NEW**



Figs. 52–60. *Arocera (Euopta) placens*. 52–54. Habitus. 55–57. Pygophore. 55. Ventral view. 56. Caudal view. 57. Lateral view. 58–60. Right paramere. 58. Lateral view. 59. Medial view. 60. Ectal view.

#### SYNONYMY.

*Arocera jalapensis* Distant, 1893:337, pl. 30, fig. 18; Lethierry and Severin, 1893: 159; Rolston, 1976:3. **NEW SYNONYMY.**

*Arocera placens*: Distant, 1900:391; Rolston, 1976:3.

*Arocera (Euopta) affinis*: Kirkaldy, 1909:109.

*Arocera (Euopta) altivola*: Kirkaldy, 1909:109.

*Arocera (Euopta) chiriquensis*: Kirkaldy, 1909:109.

*Arocera (Euopta) jalapensis*: Kirkaldy, 1909:109.

*Arocera (Euopta) patibulata*: Kirkaldy, 1909:109.

*Arocera (Euopta) placens*: Kirkaldy, 1909:110.

*Arocera (Euopta) proteus*: Kirkaldy, 1909:110.

*Arocera contralineata* Pirán, 1955:82; Becker and Grazia-Vieira, 1971:11; Grazia, 1984:73. **NEW SYNONYMY.**

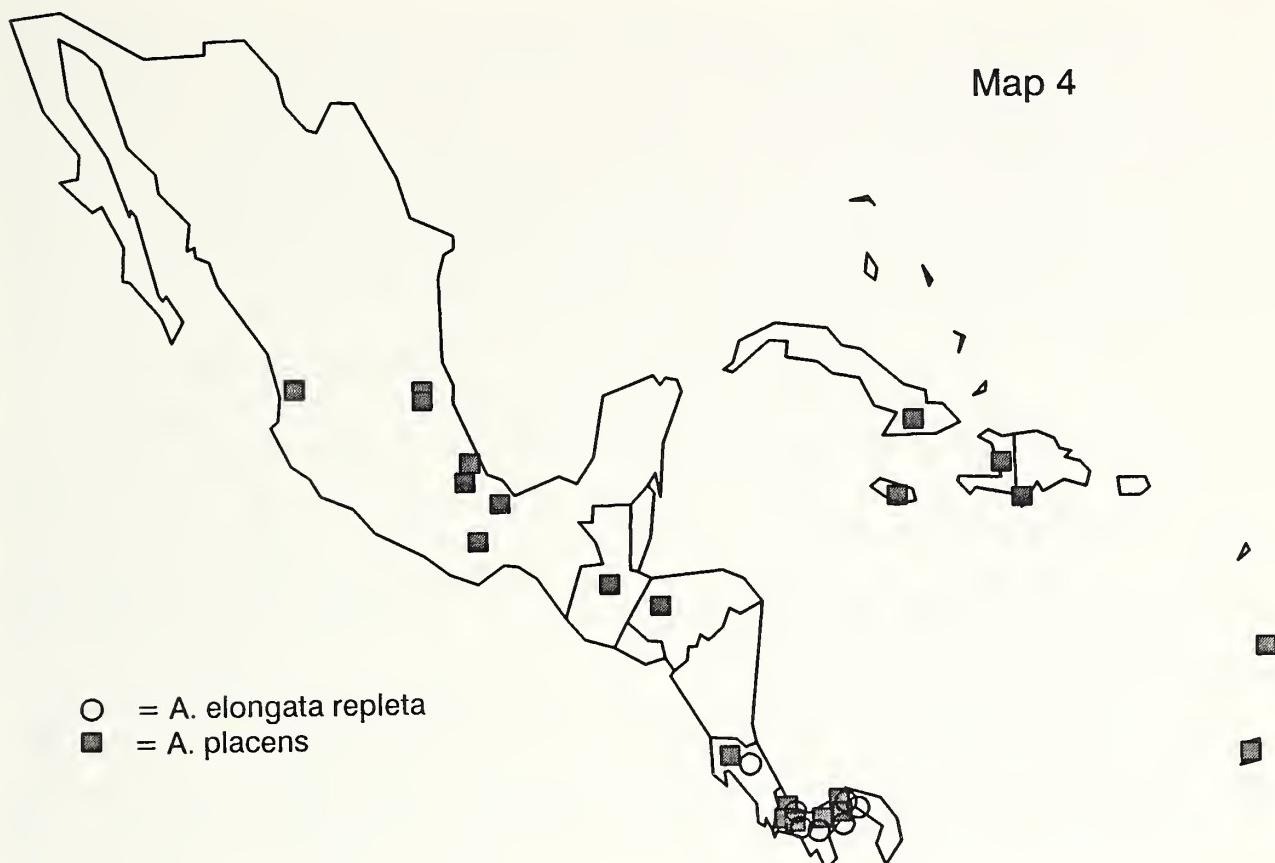
*Arocera spectabilis* (of author, not Drury): McDonald, 1984:100 (part).

*Arocera nigrorubra* (of author, not Dallas): McDonald, 1984:105–106 (part).

*Diagnosis*. Dorsal coloration extremely variable, usually yellow or orange with



Map 3. *Arocera (Euopta) apta* (○); *A. (E.) rufifrons* (▲); *A. (E.) spectabilis* (●).



Map 4. *Arocera (Euopta) elongata repleta* (○); *A. (E.) placens* (■).

brown or black macules, sometimes mostly black with yellow to red markings. Dorsal surface of head entirely black or variously marked with yellow or orange; lateral jugal margins slightly reflexed, nearly parallel, inflated apically and converging slightly over apex of tylus; jugal surfaces weakly wrinkled near base. Ocelli relatively large, each separated from adjacent eye by about its own diameter. Antennal segment I black. Ventral coloration also extremely variable. Rostral segments II-IV fuscous to black, apex extending onto base of abdomen.

Posterior margin of pygophore concave in ventral view; posterolateral angles unarmed; posteroventral surface with relatively shallow semicircular depression, ventral margin obtusely carinate (Fig. 56); weak submarginal carina parallel with posterior pygophoral margin. Each paramere in ectal view sinuously elongate, apex curving distinctly laterad with relatively shallow subapical emargination (Figs. 58, 59). Basal plates subtriangular, mesial margins nearly straight, widely separated basally, converging apically to narrowly rounded posteromesial angles, posterior margins nearly straight, transverse.

**Types.** Walker (1867) described *Strachia placens* from at least two specimens, one of which was from Santo Domingo, Hispaniola. The type specimen should be conserved at the British Museum (Natural History), but it was not located. The description, however, is adequate to fix this species.

Distant (1880, 1893) described a large number of *Arocera* species, including the following six which are examples of *A. placens*. *Arocera protea* was described from one specimen from San Gerónimo, Guatemala in 1880. The holotype was not examined, but the description with accompanying illustration and location are adequate

to fix this species. Also in 1880, he described *A. affinis* from at least four specimens from Mexico, Guatemala (San Gerónimo), and Nicaragua (Chontales) without designating a holotype or paratypes. Two ♀; syntypes were located. The specimen labeled (a) "affinis Dist." (b) "S. Gerónimo, Guatemala. Champion." (c) "Distant Coll. 1911-383." (d) "SYNTYPE" is here designated lectotype. The other specimen is here designated paralectotype and is labeled the same as the lectotype except that it lacks label (a). Both of these specimens were examined. Distant described *A. patibulata* in 1880 from Irazu, Costa Rica. McDonald (1984) considered it a junior synonym of *A. spectabilis*. However, both Distant's description and illustration indicate that the first antennal segment is black, and since this specimen is from Costa Rica it is undoubtedly *A. placens*. The holotype was not examined. In 1893, Distant described *A. altivola* from one ♀ specimen from Volcan de Chiriquí, Panama; *A. chiriquensis* from one ♂ specimen from Volcan de Chiriquí, Panama; and *A. jalapensis* from one ♀ specimen from Jalapa, Mexico. The holotype specimens for the latter species were examined. All of Distant's type material is conserved in the British Museum (Natural History), London.

Pirán (1955) described *A. contralineata* from 22 specimens with the holotype ♂ from Paso de los Libres, Corrientes, Argentina. The holotype was not located, but 20 paratypes were examined from the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires. All 20 specimens are typical specimens of *A. placens*.

*Specimens examined.* 194 specimens collected during every month of the year; deposited in AMNH, BMNH, CNC, DAR, DBT, EGER, ENGL, FSCA, LHR, MACN, OSUC, UNAM, USNM, ZMB. MEXICO: Chiapas: 30 m W San Cristóbal de las Casas. Nayarit: Tepic. Oaxaca: Oaxaca. San Luis Potosí: 24.7 m E Lauda de Matamoros, Qro; Tamazunchale; 2 m S Tamazunchale; 3 m W Xilitla. Veracruz: 25 m S Acayucan; Córdoba; El Limón; Jalapa. GUATEMALA: San Gerónimo. BELIZE: Rio Grande. HONDURAS: Lago Yojoa. COSTA RICA: Guanacaste: La Pacifica nr. Cañas. PANAMA: Boquete; Majé Stn. Bocas del Toro: Bocas del Toro; Miramar. Canal Zone: Cardenas Village; Coco Solo Hospital; Madden Dam; Pipeline Rd. Chiriquí: Fortuna; N. Candelas; Volcan de Chiriquí. Panama: Cerro Azul; Cerro Campana; Las Cumbres.

CUBA: S. Rangel; Taco Taco. JAMAICA: Hill Gardens. Clarendon: Milk River Bath. St. Andrew: Irishtown. PUERTO RICO: Ciales: 7 km S Ciales. HAITI: Laxilo. DOMINICAN REPUBLIC: Pedernales: 24 km N Cabo Rijo. ST. LUCIA. TRINIDAD: Arima Valley; Simla. Curepe: Santa Margarita Circular Rd.

COLOMBIA: Magdalena: Rio Magdalena. Putomayo: El Pueblito, Parque Nacional Tairona Sierra Nevada de S. Marta; Sta. Rosa de Sucumbios Kofan Indian Village, Rio San Miguel. Valle del Cauca: Palmira. VENEZUELA: Distrito Federal: Caracas. FRENCH GUIANA: Cayenne: Cayenne. ECUADOR: Oriente, Rio Pumayacu; Tres Cerritos. Esmeraldas: Esmeraldas. Los Ríos: Rio Palenque Biol. Stn., N of Quevedo at km 56. Napo: Coca; Shushufindi fields, 25 m N Limoncocha. Pastaza: Cuisimi, on Rio Cuisimi, 150 km SE Puyo. Pichincha: Los Banos; Quevede; 1 m W Sto. Domingo de los Colorados; Río Palenque Stn., 47 km S Sto. Domingo de los Colorados; Tinalandia, 12 km E Santo Domingo de los Colorados. PERU: Cusco: Macchu Picchu Pueblo. Huánuco: Cueva de las Pavas Cyn, 8 km S Tingo María; Tingo María. Junín: Satipo. Loreto: Iquitos, Amazon R; Explorama Lodge,

50 m NE Iquitos on Amazon R; Lake Yarinacocha, 10 km NW Pucallpa; 34 km W Pucallpa, Tournavista Rd, km 3; Rio Maraón; Yurimaguas. *Madra de Dios*: Puerto Maldonado. *San Martín*: Moyobamba region. BRAZIL: Amazonas: Benjamin Constant, Rio Javary; Manaus; 5 km N Manaus; Parintins; Tefé. Bahia: Encruzilhada. Distrito Federal: 30 km SW Brasilia. Mato Grosso: Corumbá; Sinop. Pará: Amazon R nr Obidos; Cametá. São Paulo: Est. Biol. Boracea, Salesopolis. PARAGUAY: Alto Paraguay. Central: Colonia Nueva Italia. Concepción: Horqueta, 44 km E Paraguay R. Cordillera: San Bernardino. ARGENTINA: Catamarca. Corrientes: Paso de Los Libres; Santo Tomé. Entre Ríos: Liebig. Salta: Aguas Blancas.

*Distribution.* Mexico and Cuba south to Argentina (Maps 2, 4).

*Comments.* This species is extremely variable in coloration, and some color forms are quite similar to *A. spectabilis*, *A. melanopyga*, and *A. rufifrons*. *Arocera placens* can be separated from these three species by the black antennal segment I. This species is most closely related to *A. nigrorubra* and *A. variegata* from which it can reliably be distinguished only by the male genitalia. Each paramere in ectal view is sinuously elongate with a relatively shallow subapical notch, the apex curves distinctly laterad, and the ventral margin of the pygophore is obtusely carinate. In *A. nigrorubra*, each paramere in ectal view is uniformly elongate and the apex curves only slightly laterad; while in *A. variegata*, each paramere is sinuously elongate with a relatively deep subapical notch, the apex curving distinctly laterad, and the ventral margin of the pygophore is sharply carinate.

*Arocera (Euopta) elongata elongata* Showalter, 1929  
Figs. 62–68, Map 6

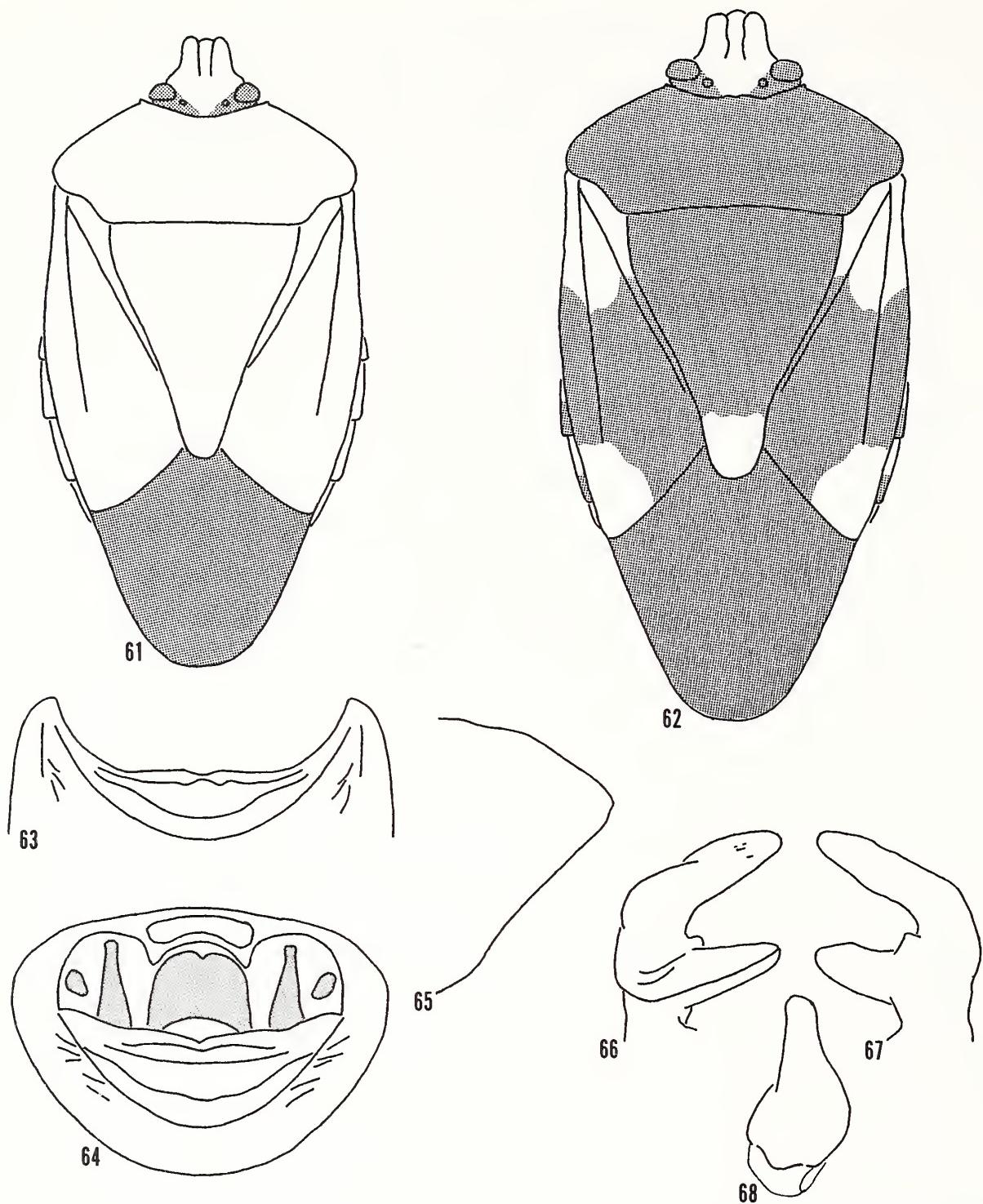
*Arocera elongata* Showalter, 1929:33, 40, pl. V; Van Duzee, 1937:25–27; Pirán, 1962: 5, fig. 4; Becker and Grazia-Vieira, 1971:11; Sabrosky, 1972:87–88; McDonald, 1984:114, figs. 56–66 (part); Grazia, 1984:73.

*Diagnosis.* Head orange except triangular area behind each ocellus black; antennae black except first segment orange. Dorsal surface black except five orange spots as follows: one occupying basal one-third of each corium; one on posterolateral angle of each corium; and one on apex of scutellum (Fig. 62), sometimes continuing cephalad as thin orange line. Anterolateral margins of pronotum straight to slightly convex.

Rostrum black except segment I orange, extending to middle of fifth (fourth visible) abdominal segment or more; legs black. Propleura completely black; ventrolateral margins of coria orange. Ventral surface of abdomen orange except segment seven and lateral portions of segment six black; genital segments black except some orange markings on genital plates of female.

Posteroventral surface of pygophore forming obtuse, semicircular carina; second, more-clearly defined submarginal carina becoming series of small wrinkles laterally; surface between carinae depressed (Fig. 63). Inferior ridge in caudal view sinuous (Fig. 64). Each paramere C-shaped with large, spatulate process near base of shaft and small tubercle just dorsal to spatulate process (Figs. 66, 67), in ectal view not curving laterad apically (Fig. 68).

*Types.* The lectotype specimen (designated by Sabrosky, 1972) was examined, and is conserved in National Museum of Natural History, Washington, D.C. The lectotype



Figs. 61–68. 61. *Arocera (Euopta) elongata repleta*, habitus. 62–68. *A. (E.) elongata elongata*. 62. Habitus. 63–65. Pygophore. 63. Ventral view. 64. Caudal view. 65. Lateral view. 66–68. Right paramere. 66. Lateral view. 67. Medial view. 68. Ectal view.

has the following label data: (a) "Oct." (b) "Chapada" and (c) "Type No. 52107 U.S.N.M."

*Specimens examined.* 88 specimens collected during every month of the year; deposited in AMNH, BMNH, CAS, CNC, DAR, DBT, EGER, ENGL, FSCA, LHR, MACN, UNAM, USNM. PANAMA: San Blas: Punta Escoses. COLOMBIA: Aguae-laro; Buena Vista. Antioquia: Jerico. Meta: Restrepo. VENEZUELA: Mérida: Mérida. ECUADOR: Oriente Zasayacu. Guayas: La Libertad. Napa: Coca; Jatun Sacha Biol.

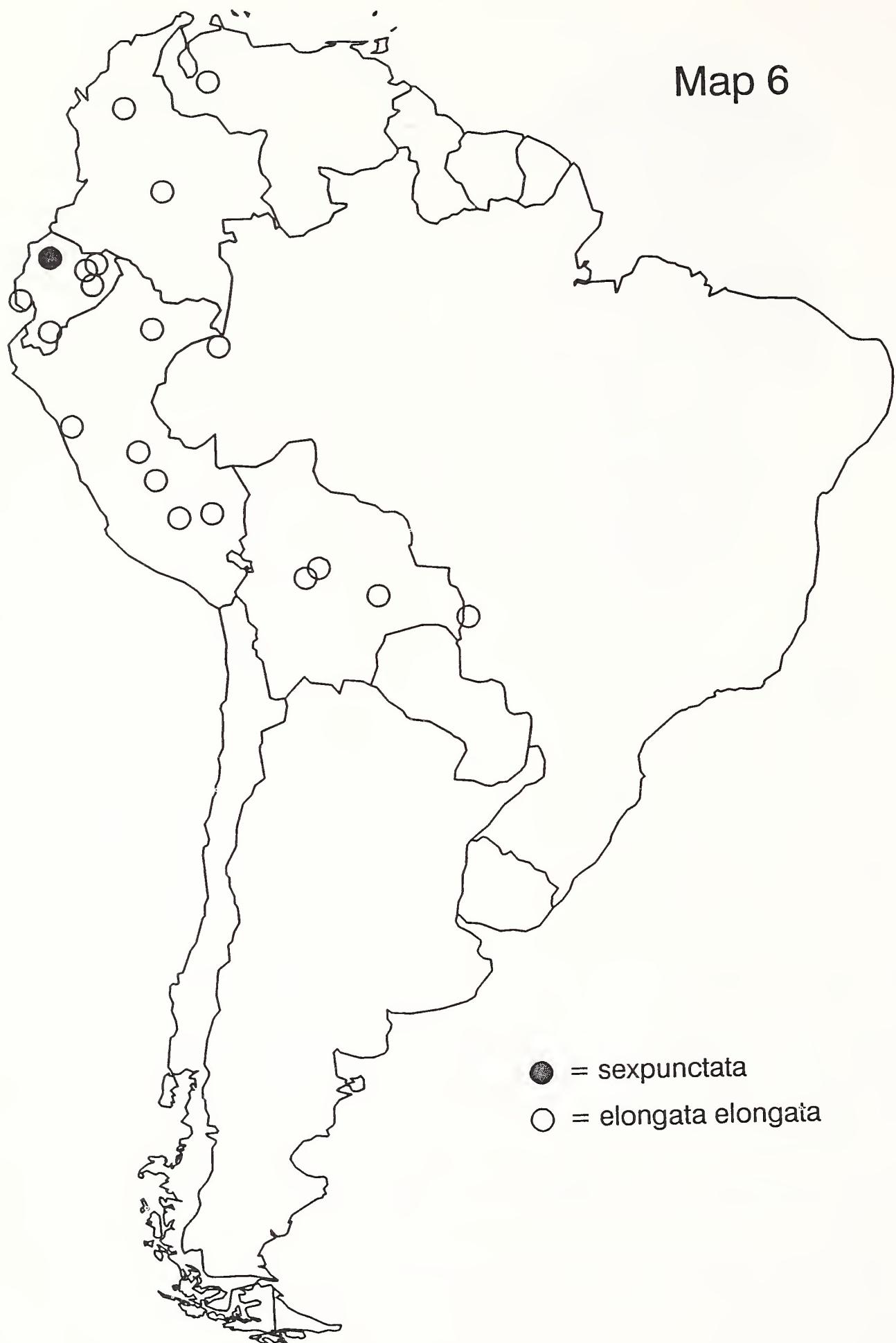


Map 5. *Arocera (Euopta) apta* (○); *A. (E.) melanopyga* (●).

Stn, 23 km E Puerto Napo; La Selva, E of Limoncocha; Limoncocha; Lumbaquí; Rd between El Puyo and Puerto Napo; Shushufindi Flds, 25 m N Limoncocha. *Pastaza*: Puyo. *Zamora-Chinchipe*: Cumbaratza; Zamora, 35 m ESE Loja. *PERU*: Montoya. *Cusco*: Macchu Picchu; Pilcopata; Quince Mil; Santa Isabel, Valley of R. Ccosnipata. *Huánuco*: Pozuzo; Tingo María. *Junín*: Prov. Jauja, Satipo; Prov. Tarma, Utcuyacu. *La Libertad*: Cumpang. above Uctubamba. *Loreto*: Middle Rio Ucayali; Pucallpa. *BOLIVIA*: Lara. *Cochabamba*: Cochabamba; Cristal Mayu, Chaparé; Palmar, Prov. Chaparé; Todos Santos, Prov. Chaparé. *Santa Cruz*: nr. Santa Cruz. *BRAZIL*: Chapada. *Amazonas*: Benjamin Constant Rio Javary. *Mato Grosso do Sul*: Corumbá.

*Distribution.* Eastern Panama and northwestern South America (Map 6).

*Comments.* Both subspecies of *A. elongata* can be readily identified by their characteristic coloration alone. *Arocera e. elongata* is black with five large orange-red spots on the dorsum, and *A. e. repleta* usually has the dorsum uniformly orange-red (except for black markings on the head and hemelytral membranes). These color



Map 6. *Arocera (Euopta) elongata elongata* (○); *A. (E.) sexpunctata* (●).

patterns are remarkably constant and are unique within the genus. The male and female genitalia of the two subspecies are identical, however, and since each seems to have distinct geographical distributions, they are best considered subspecies. *Arocera e. elongata* occurs throughout northwestern South America and eastern Panama. *Arocera e. repleta* occurs in Panama and Costa Rica.

*Arocera (Euopta) elongata repleta* Van Duzee, 1931  
Fig. 61, Map 4

*Arocera repleta* Van Duzee, 1931:94.

*Arocera elongata* (of authors, not Showalter): McDonald, 1984:114, figs. 56–66 (part).

**Diagnosis.** Dorsal surface bright orange except hemelytral membranes and triangular area behind each ocellus black (Fig. 61). Sometimes small, variable, black spots present on basal areas of pronotum and scutellum, and rarely on central area of each corium (one specimen has anterior two-thirds of scutellum and most of medial area of pronotum black). Antennae black except segment I orange. Anterolateral margins of pronotum straight to slightly convex.

Segment I of rostrum orange, remaining segments black, rostrum extending at least to middle of fifth (fourth visible) abdominal segment. Thoracic pleura black except anterolateral margins of propleura and lateral margins of meso- and metapleura orange. Legs black. Ventral surface of abdomen and genital segments as in nominate subspecies.

**Types.** The holotype specimen ♀ of *Arocera repleta* was examined. It is housed in the California Academy of Sciences, San Francisco. The holotype is type no. 3602 and is labeled from the Panama Canal Zone.

**Specimens examined.** 28 specimens collected from 13 May to 13 August; deposited in AMNH, CAS, DAR, DBT, EGER, ENGL, LHR, USNM, COSTA RICA: Puntarenas: Monteverde. PANAMA: Bocas del Toro: 2 m N divide on hwy to Chiriquí Grande; 10 km NE Fortuna Dam. Canal Zone: Barro Colorado Island; Madden Dam; Margarita. Chiriquí: Fortuna. Coclé: Cerro Gaital. Colón: Sta. Rita Ridge.

**Distribution.** Panama and Costa Rica (Map 4).

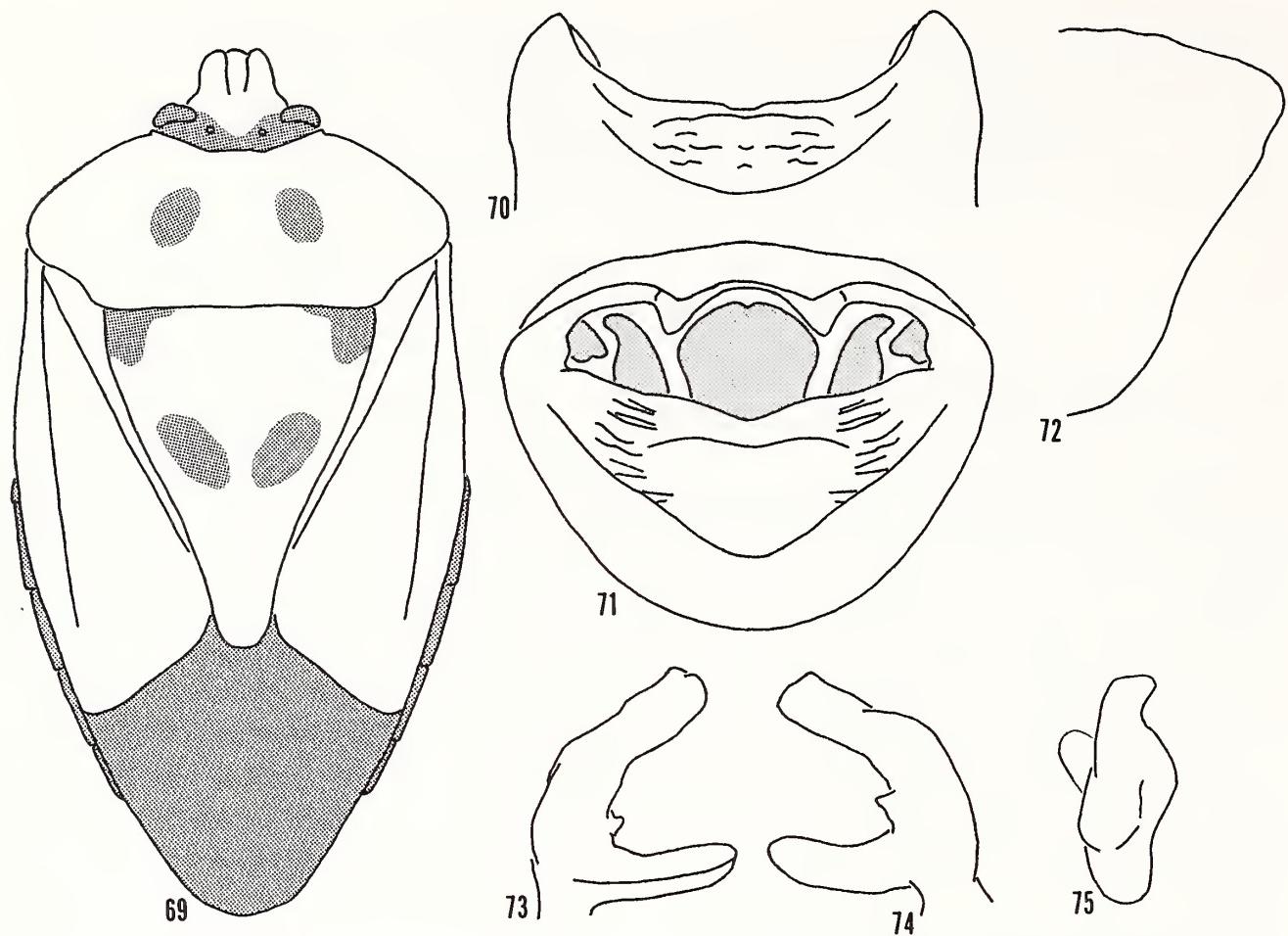
**Comments.** This subspecies can be identified by its distinctive coloration. No other species or subspecies has the dorsum uniformly orange-red as in this subspecies.

***Arocera (Euopta) sexpunctata*, new species**  
Figs. 5, 6, 19, 69–75, Map 6

*Arocera elongata* (of authors, not Showalter): McDonald, 1984:114, figs. 56–66 (part).

**Description.** Dorsal surface of head orange except triangular area behind each ocellus black. Segment I of each antenna orange, remaining segments black. Dorsal surface of body bright orange except six small black spots as follows: one in each basal angle of scutellum, one on each side of midline of pronotum just posterior to cicatrices, and one on each side of midline of scutellum about one-half distance between base and apex (Fig. 69). Anterolateral pronotal margins straight to slightly convex. Hemelytral membranes black. Connexival segments uniformly black.

Rostrum black except segment I orange, extending to middle of fifth (fourth visible) abdominal segment. Thoracic pleura black except anterolateral margins of propleura



Figs. 69–75. *Arocera (Euopta) sexpunctata*. 69. Habitus. 70–72. Pygophore. 70. Ventral view. 71. Caudal view. 72. Lateral view. 73–75. Right paramere. 73. Lateral view. 74. Medial view. 75. Ectal view.

and lateral margins of meso- and metapleura orange; ventrolateral margins of coria orange. Legs black. Abdomen completely black except some orange markings on genital plates of females.

Pygophore in ventral view with inferior ridge concave, slightly emarginate medially (Fig. 70), with submarginal semicircular depressed area wrinkled, especially laterally (Fig. 71); in caudal view inferior ridge sinuous (Fig. 71). Each paramere C-shaped with large, spatulate process near base of shaft and small tubercle just dorsad of spatulate process (Figs. 73, 74); in ectal view, paramere-head distinctly curving laterad (Fig. 75). Basal plates widely separated basally, converging distally, mesial margins convex, posteromesial angles broadly rounded, posterior margins sinuous (Fig. 19).

*Measurements.* Total length 13.72–17.35 (15.30); total width 7.89–9.30 (8.67); medial length of pronotum 2.52–3.39 (2.92). Medial length of scutellum 6.39–7.57 (6.78); basal width 5.05–5.91 (5.68); width at distal end of frena 1.89–2.37 (2.05). Length of head 2.32–2.65 (2.54); width 3.06–3.46 (3.31); intraocular width 1.60–1.88 (1.80); intraocellar width 0.91–1.11 (1.07); ocellar diameter 0.29–0.31 (0.29); distance from ocellus to adjacent eye 0.29–0.31 (0.29). Length of segments I–V of antennae 0.74–0.83 (0.83), 1.36–1.69 (1.55), 2.17–2.50 (2.32), 2.54–2.80 (2.70), and 2.37–2.58 (2.48), respectively. Length of segments II–IV of rostrum 2.70–3.24 (3.02), 3.02–3.68 (3.39), and 1.91–2.43 (2.13), respectively.

*Holotype.* ♂ labeled "ECUADOR Pichingha, 15 km E Sto. Domingo 1.XI.74 Col. J. Baier at lights." Deposited in the National Museum of Natural History, Washington, D.C.

*Paratypes.* 6♂♂, 12♀♀. Labeled as holotype (♂ 2♀♀ ENGL; ♀ LHR); labeled as holotype except "31-X-74" (♀ ENGL); (a) "Tropical rainforest general collecting" (b) "ECUADOR, Pichincha, Puerto Quito, 750m. x-xi. 1982 G. Onore" (c) "Brit. Mus. 1982-246" (4♂♂ ♀ BMNH); "ECUADOR Santo Domingo de los Colorados, Pichincha 7 February 1958 R. W. Hodges, 2000'" (♂ LHR); (a) "Ecuador Puerto Ore-llanae" (b) "Col. R. de Lafabre" (♀ UNAM); "ECUADOR: Pichincha Prov., Tinalandia 2800' elev. 12 km E of Santo Domingo June 28-30, 1980 Coll. Dan Bogar" (♀ EGER); "ECUADOR: Pichincha: Santo Domingo January 19, 1968 B. Heineman" (2♀♀ AMNH); and "ECUADOR: Pichincha Sto. Domingo de los Colorados Sept. 22, 1970 R. E. Dietz IV, leg." (2♀♀ USNM).

*Distribution.* All known specimens are from the province of Pichincha, Ecuador (Map 6).

*Comments.* Specimens of this species are very distinctively and consistently marked. No other species has a bright orange dorsal surface with small black spots as described above.

*Arocera (Euopta) rufifrons* (Dallas, 1851)

Figs. 76-82, Map 3

*Strachia rufifrons* Dallas, 1851:267; Walker, 1867:318.

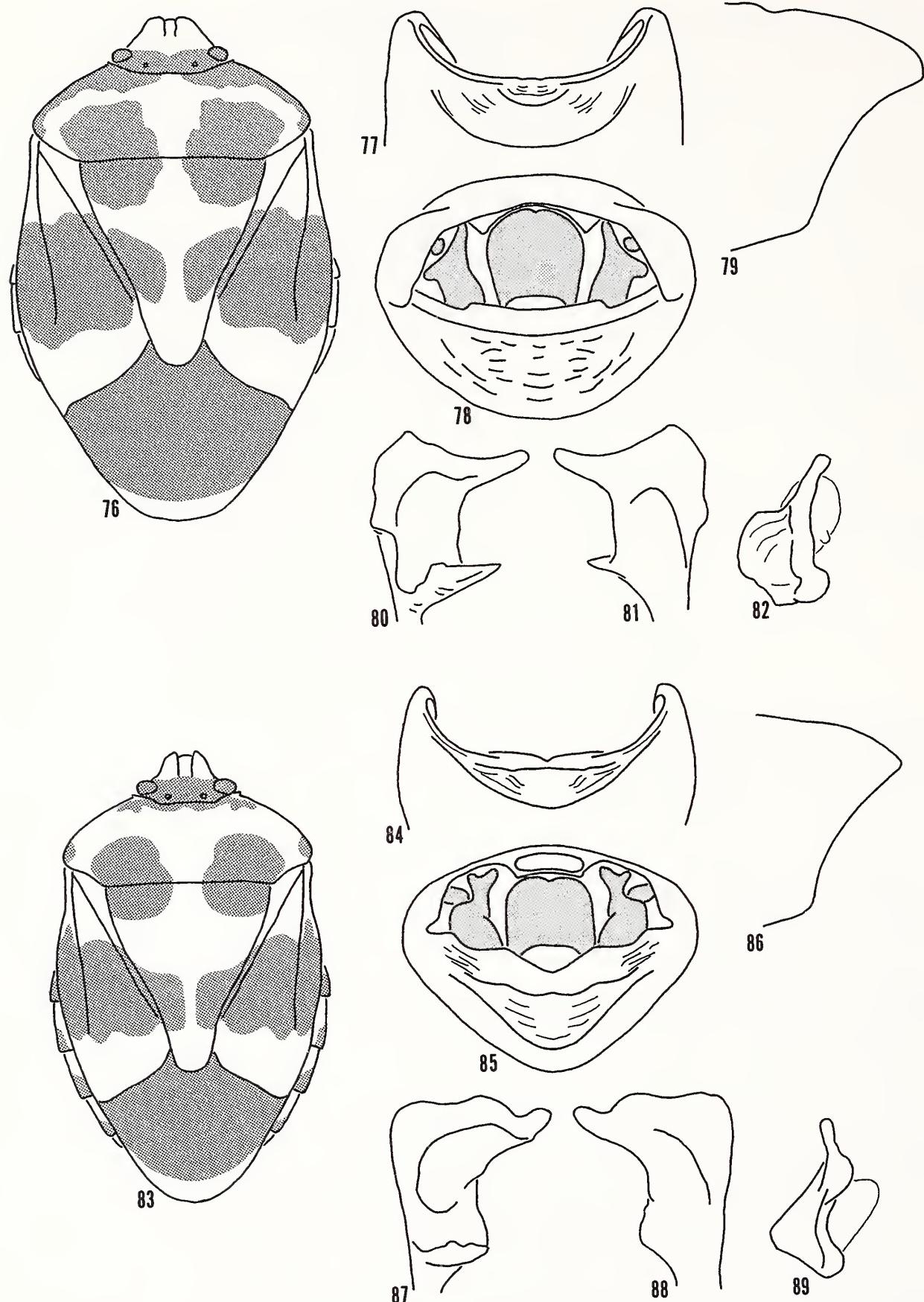
*Arocera rufifrons*: Lethierry and Severin, 1893:159; Rolston, 1976:3; McDonald, 1984:108-109, figs. 37-43 (part).

*Arocera (Euopta) rufifrons*: Stål, 1872:38; Kirkaldy, 1909:110.

*Diagnosis.* Broadly oval, dorsal coloration yellow to orange with the following black areas: basal half of head, pronotal cicatrices and area just anterior to each cicatrice, sometimes anterolateral margins of pronotum, large basal spot on each side of middle of pronotum, large spot on each basal angle of scutellum, lateral semicircular spot near apex of frenum on each side of scutellum, large spot on each hemelytron extending from scutellum to lateral margin, and hemelytral membranes except pale apices (Fig. 76).

Apex of head broadly rounded, nearly arcuate; lateral jugal margins sinuous, reflexed for most of their length; jugal apices not distinctly inflated, jugal surfaces distinctly striated. Ocelli very small, distance from each ocellus to adjacent eye at least 3-4 times diameter of ocellus. Antennal segment I pale except extreme distal end fuscous, remaining segments black. Embolium becoming distinctly wider apically, width at distal end of R + M vein at least twice basal width (Fig. 76). Corium usually appearing distinctly wrinkled in area of black spot. Connexiva uniformly yellow or orange or sometimes with black spot on each posterolateral angle.

Ventral surface of head uniformly yellow or orange. Rostrum fuscous to black, except most of segment I yellow or orange, reaching to base of fourth (third visible) abdominal segment. Ventral surface of thorax yellow to orange with large black spot on central portion of each pleuron, and usually medial areas black. Legs fuscous to black except coxae pale. Ventral surface of abdomen yellow to orange, sometimes



Figs. 76-89. 76-82. *Arocera (Euopta) rufifrons*. 76. Habitus. 77-79. Pygophore. 77. Ventral view. 78. Caudal view. 79. Lateral view. 80-82. Right paramere. 80. Lateral view. 81. Medial view. 82. Ectal view. 83-89. *A. (E.) melanopyga*. 83. Habitus. 84-86. Pygophore. 84. Ventral view. 85. Caudal view. 86. Lateral view. 87-89. Right paramere. 87. Lateral view. 88. Medial view. 89. Ectal view.

with medial black spots, especially on posterior segments, sometimes with a few irregular black spots just mesial to spiracles.

Posterior margin of pygophore in ventral view concave, sharply carinate laterally, becoming thickened and somewhat rugulose medially; posteroventral surface deeply impressed, somewhat V-shaped ventrally; ventral margin carinate laterally becoming more rounded medially (Fig. 77); inferior ridge in caudal view slightly concave with broad medial area produced slightly dorsad (Fig. 78). Parameres in medial and lateral views C-shaped, each with shaft relatively thick dorsal to basal spatulate process (Figs. 80, 81), dorsal margin broadly and shallowly concave, apex curving gently dorsad (Figs. 80, 81), basal spatulate process in nearly same plane as paramere-head (Fig. 82). Basal plates widely separated basally, converging to narrowly rounded posteromesial angles; posterior margins nearly straight with mesial areas more caudal than lateral areas.

**Types.** Dallas (1851) described *Strachia rufifrons* from an indeterminate number of specimens without designating a holotype or paratypes. McDonald (1984) located 2♀ syntypes and designated the specimen labeled 85a as lectotype, and the specimen labeled 85b as paralectotype. Both specimens were examined and are conserved in the British Museum (Natural History), London. The lectotype has the following label data: (a) "Braz." (b) "85a."

**Specimens examined.** 22 specimens collected from September to April; deposited in AMNH, BMNH, EGER, USNM, ZMB. COLOMBIA: Rio Dagus. ECUADOR: Napo: Coca; Tena PERU: Achinamiza; Chanchamayo. Huánuco: Cueva de las Pavas Cyn, 8 km S Tingo María. Loreto: Upper Rio Tapiche. BRAZIL: Guanabara, Corcovado. Amazonas: Tefé.

**Distribution.** Colombia, Ecuador, Peru, and Brazil (Map 3).

**Comments.** McDonald (1984) partially misidentified this species, including with it specimens of *A. melanopyga* from Mexico. *Arocera rufifrons*, however, is relatively rare and is restricted to northwestern South America. It may be recognized most easily by the very small ocelli and the male genitalia.

*Arocera (Euopta) melanopyga* (Stål, 1858)

Figs. 83–89, Map 5

*Strachia melanopyga* Stål, 1858:437; Walker, 1867:316.

*Arocera melanopyga*: Stål, 1861:140; Stål, 1862:107; Distant, 1880:73, pl. 7, fig. 11; Lethierry and Severin, 1893:159; Brailovsky and Barrera, 1982:237.

*Arocera (Euopta) melanopyga*: Stål, 1872:38; Kirkaldy, 1909:109.

*Arocera schumanni* Distant, 1893:336, pl. 31, fig. 17; Lethierry and Severin, 1893: 159; Rolston, 1976:3; Brailovsky and Barrera, 1982:238. NEW SYNONYMY.

*Arocera (Euopta) schumanni*: Kirkaldy, 1909:110.

*Arocera spectabilis* (of authors, not Drury): McDonald, 1984:100–102, figs. 1–8 (part).

**Diagnosis.** Dorsal surface of head smooth, yellow, except basal half fuscous to black, black not extending beyond anterior margins of eyes, often reduced with medial, narrow, longitudinal, pale line. Lateral jugal margins slightly reflexed, nearly parallel, apices of juga slightly inflated. Each ocellus relatively large, located about

its own diameter from adjacent eye. Antennae black except segment I and sometimes basal portions of segment II yellow to orange.

Dorsal surface of pronotum often with anterior margins fuscous to black, marking sometimes extending along anterolateral margins to humeral angles. Posterior disk of pronotum usually with large black spot on each side of midline (Fig. 83). Black markings on pronotum may be reduced or completely absent; black spots on posterior disk may be diffuse brown. Scutellum with black spot in each basal angle (Fig. 83). Black or fuscous trans-corioscutellar band usually present (Fig. 83), but may be reduced and interrupted by thin, pale, line on middle of scutellum and sometimes on coria. Hemelytral membranes fumose except apical margins pale (Fig. 83). Connexival segments yellow to orange, usually with fuscous to black spots in posterolateral angles (Fig. 83).

Ventral surface of head yellow to orange. Rostrum usually fuscous to black except segment I yellow to orange, sometimes orange markings also on segments II–III, extending to anterior margin of fourth (third visible) abdominal sternite. Coloration of thoracic pleura variable ranging from yellow or orange to fuscous to black on extensive areas of meso- and metapleura, propleura rarely with black markings. Legs with varying amounts of fuscous and pale areas. Abdominal sternites sometimes uniformly pale, but usually with black spots laterally and sometimes along midline.

Posterior margin of pygophore in ventral view concave, sinuous medially (Fig. 84); in caudal view inferior ridge sinuously V-shaped; posteroventral surface wrinkled, with V-shaped depressed area (Fig. 85). Each paramere flat, thin; apex undulating, appearing tri-lobed; in lateral and medial views, lobes not as distinct as in *A. spec-tabilis* (Figs. 87, 88); basal spatulate process nearly perpendicular to paramere-head (Fig. 89). The female genitalia are typical for the subgenus.

*Types.* Stål (1858) described *Strachia melanopyga* from at least two female specimens from Mexico. The type material is probably deposited in the Naturhistoriska Riksmuseet, Stockholm, Sweden, but the specimens were not located. This species can, however, be fixed by Stål's original description and its type locality. *Arocera melanopyga* is the only known species occurring in Mexico that has the first antennal segment pale.

Distant (1893) described *A. schumannii* from 2♂ and 2♀ specimens without designating a holotype or paratypes. The ♂ specimen labeled (a) "Tepic, Mex. July. Schumann." (b) "B. C. A., Hem. 1. Arocera schumannii" (c) "SYNTYPE" is designated lectotype. The remaining specimens are designated paralectotypes and have the following label data: (a) "schumannii Dist." (b) "Tepic, Mex. July. Schumann." (c) "Distant Coll. 1911-383." (d) "SYNTYPE" (♂); (a) "Tepic, Mex. July. Schumann." (b) "Distant Coll. 1911-383." (c) "SYNTYPE" (♀); (a) "Tepic, Mex. July. Schumann." (b) "B. C. A., Hem. 1. Arocera schumannii" (c) "SYNTYPE" (♀). All four specimens were examined; in important characters of the male and female genitalia they do not differ significantly from *A. melanopyga*. The specimens are conserved in the British Museum (Natural History), London.

*Specimens examined.* 50 specimens collected from 19 April to 9 October; deposited in BMNH, CAS, DAR, DBT, EGER, LHR, UNAM. MEXICO: Chiapas: Aguacero; Chicoasen Dam Area; Parque Laguna Belgica, 12 m N Ocozocuatla; 20 km NE Tuxtla Gutierrez. Guerrero. Jalisco: Estación de Biología "Chamela", 8 km S Chamela. Nayarit: 8.7 m E San Blas; Tepic. Oaxaca: Palomeres. Quintana Roo: Bacalar;

Nuevo, X-Can. *Tamaulipas*: Bocatoma, 6 m S Gomez Farias; 8 m W El Limon; 73.1 m N Manuel. *Veracruz*: Los Tuxtlas; 15.8 m S Tampico. BELIZE: Orange Walk Town. GUATEMALA: Cayuga; Escuintla Peñon de Siquinala.

*Distribution.* This species occurs in Mexico and northern Central America (Map 5).

*Comments.* This species has recently been considered a junior synonym of *A. spectabilis*, from which it is geographically isolated. Specimens of *A. spectabilis* are consistently marked, whereas *A. melanopyga* is extremely variable.

*Arocera melanopyga* is most similar in coloration to *A. rufifrons* and *A. apta*, both of which occur only in South America. It differs from both of these species by the lack of black markings on the propleura and by the male genitalia. It further differs from *A. rufifrons* by the large ocelli. The ocelli are very small in *A. rufifrons*.

The only similarly colored sympatric species is *A. placens*, which can be separated by the male genitalia and the color of antennal segment I. The first antennal segment is pale in *A. melanopyga* but black in *A. placens*.

*Arocera (Euopta) spectabilis* (Drury, 1782)

Figs. 11–14, 90–96, Map 3

*Cimex spectabilis* Drury, 1782: index, 66, pl. 46, fig. 4.

*Strachia spectabilis*: Dallas, 1851:266; Stål, 1860:22; Walker, 1867:318.

*Strachia generosa* Stål, 1854:233; Walker, 1867:317 [synonymized by Stål, 1872].

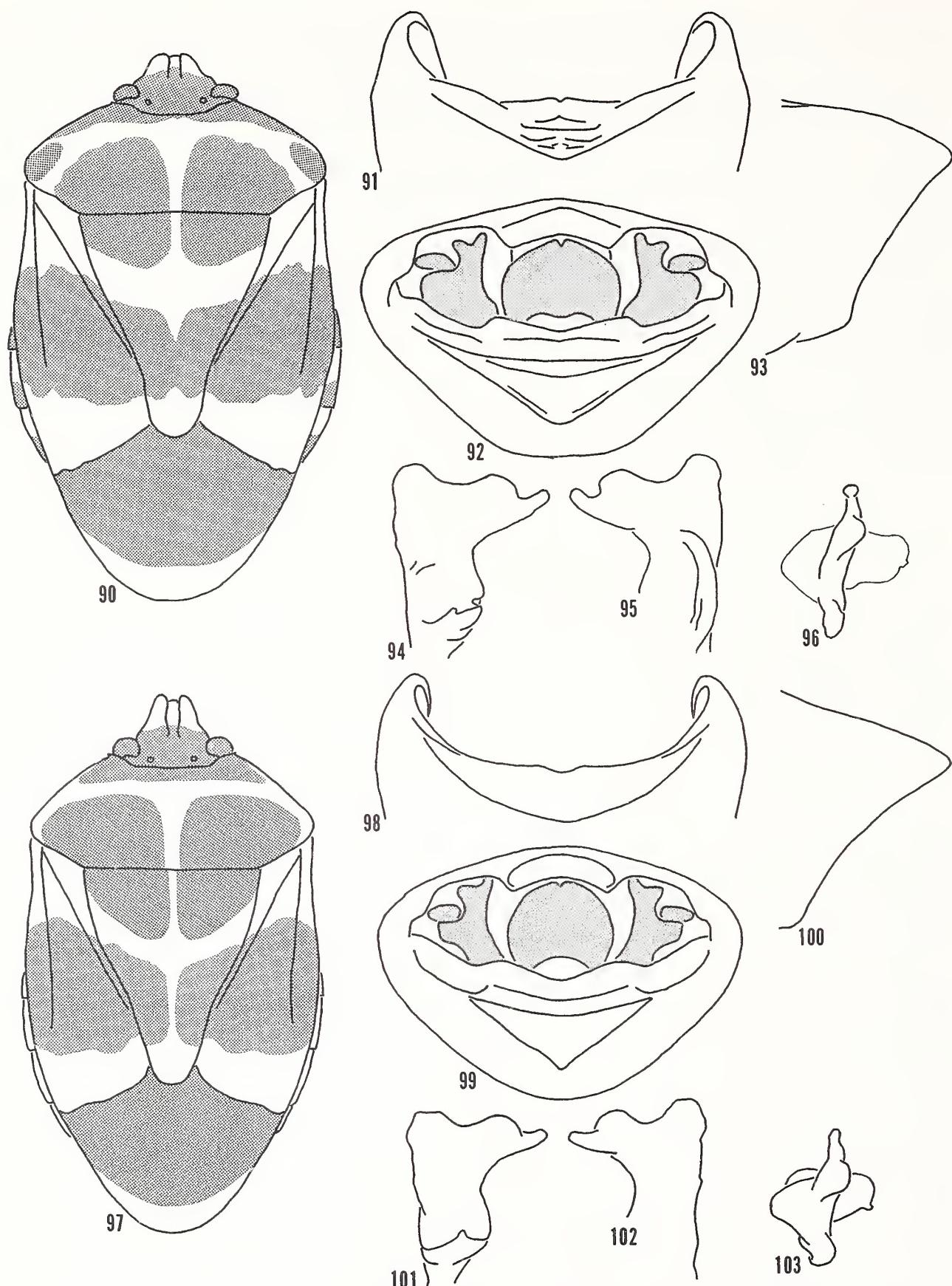
*Arocera spectabilis*: Stål, 1861:140; Lethierry and Severin, 1893:159; Grazia, 1977: 163; McDonald, 1984:100–102; figs. 1–8 (part).

*Arocera (Euopta) spectabilis*: Stål, 1872:38; Kirkaldy, 1909:110.

*Diagnosis.* Dorsal surface of head weakly wrinkled near base of juga, with apical portion orange-red, basal portion black; black usually extending onto basal areas of juga and tylus (Fig. 90). Juga distinctly inflated apically; lateral margins reflexed, sinuous, tapering to truncately rounded apex. Antennae black except segment I red-orange; ocelli relatively large, each located about its own diameter from adjacent eye.

Anterior margin of pronotum black except yellow intruding medially to anterior reflexion; anterior black areas usually extending along anterolateral margins, then forming distinct black spot on each humeral angle (Fig. 90). Large black spot on each side of midline of posterior pronotal disk, extending onto base of scutellum. Broad black band traversing coria and scutellum near middle of scutellum (Fig. 90), sometimes divided on midline of scutellum by thin yellow line (Fig. 90). Hemelytral membranes black, apical margins transparent (Fig. 90). Connexia red-orange with large black spot in each posterolateral angle. Anterolateral pronotal margins nearly straight; hemelytra lacking wrinkles. Embolium somewhat widened apically.

In ventral view, posterior margin of pygophore concave, slightly sinuous (Fig. 91); weak submarginal carina parallel to posterior margin; posteroventral surface of pygophore with broad V-shaped depression, ventral margin obtusely carinate (Fig. 92). Each paramere undulating dorsally, apex curving dorsad slightly more than in *A. apta*, with large spatulate process near base protruding laterad, perpendicular to paramere-head (Fig. 96) with small rectilinear tubercle apically (Fig. 94); subtriangular, flattened, dorsal margin appearing tri-lobed in lateral and medial views (Figs. 94, 95). Basal plates widely separated basally, converging apically; mesial margins



Figs. 90–103. 90–96. *Arocera (Euopta) spectabilis*. 90. Habitus. 91–93. Pygophore. 91. Ventral view. 92. Caudal view. 93. Lateral view. 94–96. Right paramere. 94. Lateral view. 95. Medial view. 96. Ectal view. 97–103. *A. (E.) apta*. 97. Habitus. 98–100. Pygophore. 98. Ventral view. 99. Caudal view. 100. Lateral view. 101–103. Right paramere. 101. Lateral view. 102. Medial view. 103. Ectal view.

convex, posterior margins nearly straight, posteromesial angles rounded slightly prominent.

*Types.* The type of *Cimex spectabilis* was not located, but this species is easily fixed by the illustrations of Drury (1782).

I was not able to examine any of the type material of *Strachia generosa*, but since Stål (1872) himself placed his species as a junior synonym of *A. spectabilis* I have followed this synonymy.

*Specimens examined.* 72 specimens collected from 6 August to 12 March; deposited in AMNH, EGER, UNAM, USNM, ZMB. BRAZIL: E. Bresslau; Guapi; Laguna Aztezca, Holango, Hidalgo. Bahia: Encruzilhada; Rio, v. olfers, Sello. Esperito Santo: Conceição da Barra. Minas Geraes: Diamantina; Pedra Azul; Viçosa. Pernambuco: Tapera. Rio Grande do Norte: Natal. Rio de Janeiro: Petrópolis; Rio de Janeiro. Rio Grande do Sul: Pelotas; Pôrto Alegre. Santa Catarina: Corupa; Rio Natal. São Paulo: Casa Grande, Boraceia Field Stn.

*Distribution.* Southern and eastern Brazil (Map 3).

*Comments.* This species resembles some specimens of *A. placens* from which it may be separated by the pale first antennal segment; the first antennal segment is black in *A. placens*. It is most closely related to *A. apta*, which in fact may be a subspecies of this species. The genitalia of the two are very similar, but the differences in coloration are distinct and constant. *Arocera spectabilis* always has black markings on the humeral angles, the connexiva, and the abdominal venter. These markings are never present in *A. apta*.

*Arocera (Euopta) apta* (Walker, 1867)

Figs. 97–103, Maps 3, 5

*Strachia apta* Walker, 1867:323.

*Arocera crucigera* Haglund, 1868:157; Lethierry and Severin, 1893:159; Froeschner, 1981:68. **NEW SYNONYMY.**

*Arocera (Euopta) crucigera*: Stål, 1872:38; Kirkaldy, 1909:109.

*Arocera apta*: Distant, 1880:73, pl. 7, fig. 12; Distant, 1893:336; Lethierry and Severin, 1893:159; Pirán, 1963:107; Rolston, 1976:3; Becker and Grazia-Vieira, 1977: 55; Froeschner, 1981:68; Grazia, 1984:73.

*Arocera (Euopta) apta*: Kirkaldy, 1909:109.

*Arocera malonopyga* [sic] (of authors, not Stål): Pirán, 1956:29.

*Arocera melanopyga* (of authors, not Stål): Pirán, 1962:6.

*Diagnosis.* Dorsal coloration very similar to *A. spectabilis*, ground color yellow with six large black macules: one on basal half of head extending onto anterior margin of pronotum, one on each side of midline of posterior pronotal disc continuing onto basal areas of scutellum, one on each corium near middle extending onto scutellum near distal end of frenum, and one consisting of black hemelytral membranes (Fig. 97). Black on basal half of head extends at most only slightly onto basal areas of juga; black markings entirely absent from humeral angles (Fig. 97). Connexiva entirely pale yellow. Dorsal punctuation minute and very sparse.

Lateral jugal margins slightly reflexed, sinuous, nearly parallel, extending slightly beyond apex of tylus; jugal surfaces weakly wrinkled. Antennae black except segment I and sometimes basal portion of segment II pale. Each ocellus relatively large,

separated from adjacent eye by about its own diameter. Ventral surface yellow except for one black macule on middle of each pleurite. Rostrum yellow except segment IV black, usually extending onto fourth (third visible) abdominal sternite; legs black except basal half of each femur yellow.

Pygophore with posterior margin in ventral view concave, slightly emarginate medially (Fig. 98), posteroventral surface with shallow, submarginal, triangular, depressed area (Fig. 99); inferior ridge in caudal view sinuous (Fig. 99). Each paramere undulating, trilobed dorsally, apex not curving dorsad as much as in *A. spectabilis*, with large spatulate process near base of paramere protruding laterad (Fig. 101), nearly perpendicular to paramere-head (Fig. 103). Female genitalia typical for subgenus.

**Types.** Walker (1867) described *Strachia apta* from an indeterminate number of specimens from Brazil without designating a holotype or paratypes. Only 1 ♀ syntype was located and is here designated the lectotype. It has the following label data: (a) "62 57" [dorsal surface], "Braz" [ventral surface] (b) "Type" (c) "41. STRACHIA APTA." [dorsal surface] "nereous, with black Ve" [ventral surface] (d) "68." This specimen was examined and is housed in the British Museum (Natural History), London.

The type material of *Arocera crucigera* Haglund should be deposited in the Naturhistoriska Riksmuseet, Stockholm, Sweden, but no specimens were located. McDonald (1984) examined the holotype and considered *A. crucigera* to be a junior synonym of *A. spectabilis*. The type locality of the Brazilian Amazon more likely places it in the known distribution of *A. apta*.

**Specimens examined.** 173 specimens collected from every month of the year; deposited in AMNH, BMNH, CAS, CIAT, CNC, DAR, DBT, EGER, ENGL, FSCA, LHR, MACN, OSUC, UNAM, USNM, ZMB. COSTA RICA: Esparta; Turrialba. Heredia: 1 km S Pt. Viejo. Puntarenas: Finca Las Cruces, 6 km S San Vito de Java; Las Cruces, 7 km S San Vito; Palmar. PANAMA: Gamboa; Punta Vacamonte, 8°52'N 79°40'W. Bocas del Toro: 2 mi N Divide on hwy to Chiriquí Grande; Miramar, 9°N 82°15'W. Canal Zone: Barro Colorado Island; Coco Solo Hospital; Ft. Gulch; Ft. Gulion. Chiriquí: Renacimiento Santa Clara; Volcan de Chiriquí. Coclé: Cerro Gaital. Colón: Santa Rita Ridge. Darien: 23 km E Cañanzas. Panama: Altos de Majé, Chepo; Cerro Campana; ~10 km N El Llano; Las Cumbres.

COLOMBIA: Amazonas: Leticia. Antioquia: Medellín. Atlántico. Caquetá: Rio Orteguaza nr Rio Peneya. Meta: Pto. Gaitón-Carimagua; Restrepo. Valle de Cauca: Buenaventura. VENEZUELA: Río Chaurito. Amazonas: San Carlos de Ríos Negro. Aragua: Rancho Grande. Carabobo: Valencia. Distrito Federal: Caracas. Mérida: Hwy to El Vigía. Yaracuy: Aroa. GUYANA: Essequibo R., Moraballi Crk; East Berbice-Corentyne: Oronoque & New River heads. Mazaruni-Potaro: Bartica District, Penal Settlement; Kartabo Point; Takutu Mtns. FRENCH GUIANA: Cayenne: Cayenne; Hwy D6 to Kaw, 34 km SE Roura; Hwy N2 to Regina, 45 km S Cayenne; Hwy N2 to Regina, 67 km S Cayenne. St. Laurent du Maroni: St. Jean; Hwy ext. N1, 20 km SE St. Laurent; 13 km SSE St. Laurent. ECUADOR: Salidoro. Azuay: Sta. Isabel, 65 km SW Cuenco. El Oro: Santa Rosa; W of Santa Rosa, just S of Machala. Esmeraldas: San Mateo. Guayas: Guayaquil. Los Ríos: Pichilingue Expt Stn, Quevedo; Río Palenque. Manabí: Prov. Penchancha, 8 km N Tinalandia, Sto. Domingo de los Colorados. Napo: Coca; La Selva; Limoncocha, on Río Napo; Lumbaqui Stn, 70 km W Lago Agrio. Pastaza: Puyo; 16 km W Puyo. Pichincha: Puerto Quito; Sto. Domingo

de los Colorados; Río Palenque Stn, 47 km S Sto. Domingo de los Colorados; Tinalandia, 12 km E Sto Domingo de los Colorados; 15 km E Sto. Domingo de los Colorados. PERU: Achinamiza. Amazonas: Río Santiago. Cusco: Pilcopata; Prov. Paucartambo, Haciendo María, Shores of Río Ccosnipata. Huanuca: Tingo María. Junín: Prov. Tarma, Utcuyacu. La Libertad: Cumpang. above Uctubamba. Loreto: Callicebus Res. Stn. Mishana, Río Nanay, 25 km SW Iquitos; Guyabamba, 3 kms from Iquitos; Iquitos, Platanal; middle Río Ucayali; Requena. Madre de Dios: mouth La Torre River; Río Tambopata Reserve, 30 km SW Puerto Maldonado. San Martín: El Boquerón Pass; Río Huallaga. Ucayali: Pucallpa; 34 km W Pucallpa; 3 km NE Abra Diuisoria on Tingo-María-Pucallpa hwy. BOLIVIA: Sara; S. F. Chipiriri. Cochabamba: Chaparé, Alto Palmar; Chaparé, Villa Tunari. El Beni: Blancaflor; Riberalta; Rurrenabaque. La Paz: Ixiamas. Santa Cruz: Buena Vista, Proc. Ichilo; Colpa Gas P. Stn, 9 mi W Warnes; 10 mi W Portachuelo; Santa Cruz. BRAZIL: Amazonas: Amazons between Pará and Manaus; Benjamin Constant, Río Javary; Hyutanahan, Río Purus; Manaus; 5 km N Manaus; 244 km Manaus; Uypiranga Río Negro, 14 km from Manaus; Puraquequara; São Paulo de Olivença; Tefé. Bahia: Río, v. olfers, Sello. Mato Grosso: 10°25'S, 59°28'W; Sinop. Mato Grosso do Sul: Corumbá. Pará: Almeirim, São Raimundo; 330 m S Belém; Jacaréacanga; Santarém; Urúa, 65 km SW Itaituba on BR 230. Rondônia: Porto Velho. Santa Catarina: Río Vermelho. ARGENTINA: Salta: San Martin Palitos.

*Distribution.* Costa Rica to Brazil (Maps 3, 5).

*Comments.* This species is similar in appearance to some specimens of *A. placens* but differs from that species by the pale first antennal segment. It is also closely related to *A. melanopyga*, but *A. apta* is very consistently marked, whereas *A. melanopyga* is extremely variable. The two are also geographically isolated, with *A. melanopyga* restricted to Mexico and northern Central America, and *A. apta* occurring from Costa Rica southward into much of South America. *Arocera apta* is also similar to *A. rufifrons* but can be separated from that species by its larger ocelli and usually by the yellow ground color. *Arocera rufifrons* has very small ocelli, and the ground color is usually orange.

This species is most closely related to *A. spectabilis* and may only be a subspecies of that species. The genitalia of the two species are very similar, but the differences in coloration are distinctive and consistent. *Arocera spectabilis* always has black markings on the humeral angles, the connexiva, and the abdominal sternites; these markings are always absent in *A. apta*.

#### NOMINA DUBIA

##### *Arocera fasciativentris* Breddin, 1901

*Arocera fasciativentris* Breddin, 1901:139; Kirkaldy, 1909:367; McDonald, 1984:118 [*nomen dubium*].

*Arocera fasciativentris* Breddin was described from Rio Grande do Sul, Brazil. McDonald (1984) listed this species as a *nomen dubium* as he was not able to locate any type material and it is not possible to fix the species from the description. He speculated that it was probably a junior synonym of *A. spectabilis*. The description does match *A. spectabilis* fairly well, except that Breddin indicates that the antennae are black. This suggests that *A. fasciativentris* may be a junior synonym of *A. placens*.

*Arocera capitata* Breddin, 1901

*Arocera capitata* Breddin, 1901:139; Kirkaldy, 1909:367; McDonald, 1984:118 [*nomen dubium*].

McDonald (1984) also listed this species as a *nomen dubium* and suggested that it was a junior synonym of *A. spectabilis*. Once again, its description fits *A. spectabilis* fairly well, but its type locality of Bolivia places it well outside the range of *A. spectabilis*. Breddin mentions that the eyes are unusually small. I have not seen any specimens in which the compound eyes are small, but *A. rufifrons* has very small ocelli, and if Breddin was actually referring to the ocelli, then *A. capitata* is probably a junior synonym of *A. rufifrons*.

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**DESCRIPTION OF THE MALE OF *OXYPORUS BALLI*  
CAMPBELL, WITH NOTES ON DISTRIBUTION OF  
*OXYPORUS* IN MEXICO  
(COLEOPTERA: STAPHYLINIDAE)**

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*Abstract.*—The male of *Oxyporus balli* Campbell is described for the first time, based on specimens collected in Morelos, México. Conspecific females collected in the same locality differed in color. The host mushrooms for *O. balli* are recorded for the first time: *Amanita caesarea* and *A. rubescens*. New records and host mushroom for *O. mexicanus* Fauvel and *O. lawrencei* Campbell are included.

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The original description of *Oxyporus balli* by Campbell (1969) was based on two females collected in the Mexican states of Michoacan and Morelos. The purpose of this paper is to describe the male of *O. balli* and comment on color pattern variation in females, all collected recently in Morelos.

*Oxyporus balli* Campbell, 1969  
Can. Entomol. 101:254

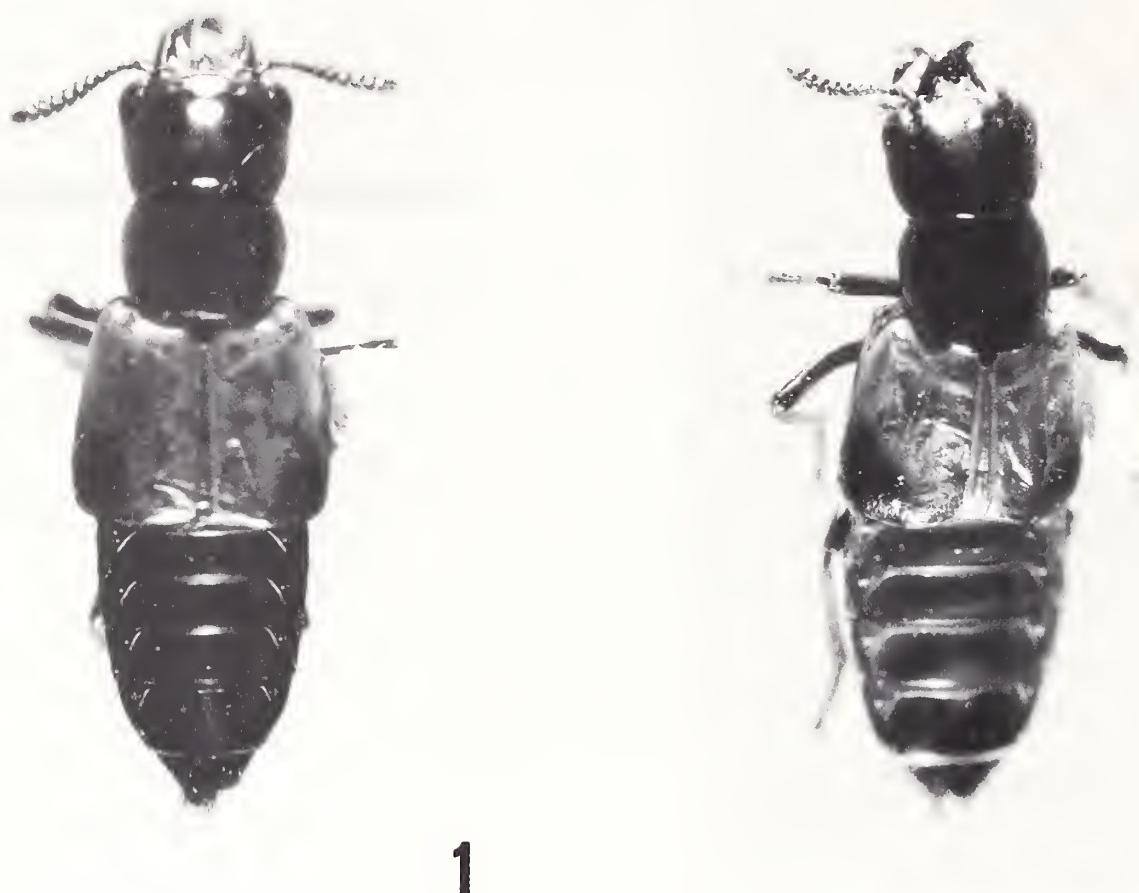
*Description of male.* Black but labrum and tarsi light yellow, elytra (except broad vitta on extreme outer apical angles) bright yellow.

Head quadrate to slightly transverse, its width (including eyes) slightly broader than width of pronotum; temples shorter than eyes. Frons near to clypeus with two depressions between antennae. Anterior margin of clypeus slightly emarginate medially. Mandibles shorter than length of head, with deep depression close to base; left mandible with two teeth near middle to receive right mandible, one directed ventrally and one medially; each mandible slightly curved with acute apex.

Thorax with pronotum slightly wider than long, widest near anterior margin, gradually narrowed to base. Suture between mesepisternum and mesepimeron slightly carinate. Tarsi slender, lacking fine setae ventrally; first tarsomere shorter than second, fifth longest.

Abdomen with tergite VIII and sternites VII and VIII moderately densely covered with long setae near posterior margin; other sternites with row of long setae sparsely placed near posterior margin. Aedeagus (Fig. 5) with broad median lobe, its apex broadly rounded; parameres without apical setae.

*Material examined.* MEXICO: Morelos, Tlayacapán, San José de los Laureles, 3.VI.1990, cols. J. L. Navarrete y G. A. Quiroz, ex *Amanita caesarea*, #283, *Oxyporus balli* Campbell, Det. J. L. Navarrete 1990, (1♀); same data except for: ex *Amanita rubescens*, 05.VIII.1990, #440 (1♂, 1♀); same data except for: 06.VIII.1990, #453,



Figs. 1, 2. Dorsal habitus. 1. *Oxyporus balli* Campbell, male. 2. *O. balli*, female.

(1 ♂). Specimens are deposited in my personal collection, and in the Canadian National Collection.

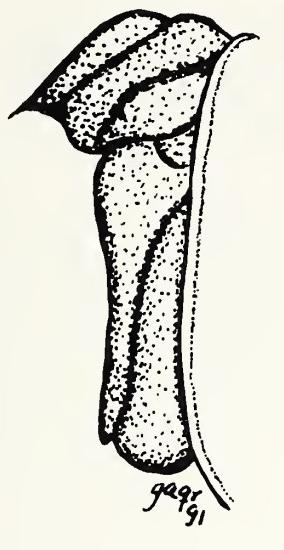
*Distribution.* Known only from Michoacan and Morelos at high altitude. The specimens examined were collected at 1,700 m.

*Habitat and habits.* The specimens examined were collected from two species of *Amanita* in a cloud forest, in June and August.

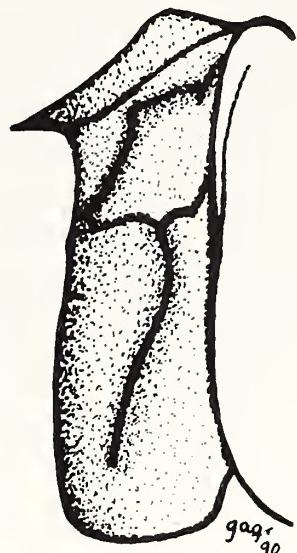
*Remarks.* The color pattern of the two females examined differs from that described by Campbell (1969) as follows: the metasternum, mesepimeron, metepisternum, metepimeron and sternites I–V are yellow; tergites III–VI are yellow with black spots at lateral margins; in one female, the hind legs are mostly yellow except for a small black spot near the apex of the femur. Male and female habitus and color pattern are illustrated in Figures 1–2. This species resembles *O. rufipennis* LeConte from eastern North America, however it differs primarily in having the extreme outer apical angles of the elytra black, the elytral epipleura inconspicuous, the mesepisternum broader (Figs. 3, 4), and by differences in the aedeagus (Figs. 5, 6).

#### NEW MEXICAN DISTRIBUTIONAL RECORDS FOR *OXYPORUS*

*O. lawrencei* Campbell is known from Eslava (Distrito Federal), Sierra de Taxco (Guerrero), and Derrame del Chichinautzin (Morelos) (Campbell, 1974; Navarrete-Heredia and Novelo-Gutiérrez, 1990). The following label data provide new records



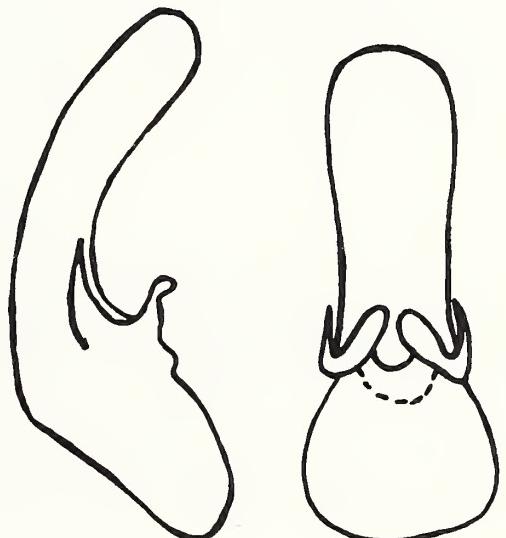
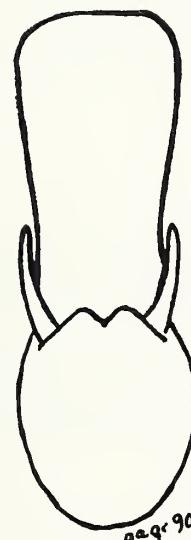
3



4



5



6

Figs. 3–6. *Oxyporus* spp. 3, 4: Pterothorax, lateral view. 3. *O. balli*. 4. *O. rufipennis* LeConte. 5, 6: Aedeagus, lateral and ventral views, respectively. 5. *O. balli*. 6. *O. rufipennis*.

for an additional state: MEXICO: México, San Rafael, cerca "casetas," 09.IX.1989, col. J. L. Navarrete, *ex* hojarasca, cerca de hongos, *Oxyporus lawrencei* Campbell, Det. J. L. Navarrete 1989, (1); km 14–17 carr. Cuernavaca-Ocuilán, 27.VII. 1990, *ex* hojarasca, cerca de *Tricholoma* sp., #408, *Oxyporus lawrencei* Campbell, Det. J. L. Navarrete 1990, (1).

*O. mexicanus* Fauvel is known from Durango, Guerrero, Oaxaca and Morelos (Campbell, 1969; Navarrete-Heredia and Novelo-Gutiérrez, 1990). The following label data provide additional habitat information: MEXICO: Morelos, Tlayacapán, San José de los Laureles, 3.VI.1990, cols. J. L. Navarrete y G. A. Quiroz, *ex Amanita caesarea* #277, *Oxyporus mexicanus* Fvl., Det. J. M. Campbell (4); same data except for, #283, Det. J. L. Navarrete (3).

#### REMARKS

Scheerpeltz (1960) described *O. boliviensis* from Bolivia; the female type is deposited in Munich (A. F. Newton, pers. comm.). This species was excluded from Campbell's (1969) revision. Scheerpeltz (1960) also cited questionable locality records for various Mexican species: for *O. smithi* Bernhauer and *O. guerreroanus* Bernhauer, Iguala and Tapantitlan (also cited as Tepantitlan) (the first locality is in Guerrero and the latter is without precise geographic locality); for *O. mexicanus* Fauvel and *O. flohri* Sharp, Juquila in Oaxaca; and for *O. fenyesi* Bernhauer (=*O. mexicanus*), Toluca, the capital of the Estado de Mexico.

The type series of *O. flohri* was originally collected by Flohr at "Alto del Tizar," a questionable locality in Mexico (see Campbell, 1990). Campbell suggested that this locality is probably in the mountainous areas of Chiapas. Recently, Biol. L. Delgado (Instituto de Ecología) discovered a locality named "Alto del Tizar" in the Mexican state of Veracruz, near to Naolinco. It is possible this "Alto del Tizar" is the true type locality of *O. flohri*. If confirmed as such, this geographic locality will represent the first record of an *Oxyporus* from eastern Mexico.

#### ACKNOWLEDGMENTS

The author acknowledges Biol. G. A. Quiroz-Rocha for her help with the line drawings and her company during collecting trips. Drs. J. H. Frank (University of Florida, Gainesville), J. M. Campbell (Biosystematics Research Centre, Ottawa), and A. F. Newton, Jr. and M. K. Thayer (Field Museum of Natural History, Chicago) kindly reviewed an earlier draft of the manuscript. Mr. L. Delgado (Instituto de Ecología) discovered and informed me of the "Alto del Tizar" locality in Veracruz. I also thank M. J. A. Hernandez G. (Lab. de Microcine, Fac. de Ciencias) for preparation of the habitus photographs.

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Campbell, J. M. 1974. A new species of *Oxyporus* (Coleoptera: Staphylinidae) from Mexico with comments on *Oxyporus elegans* LeC. Coleopts. Bull. 28:155–157.  
Campbell, J. M. 1990. A new species of *Oxyporus* (Coleoptera: Staphylinidae) and rediscovery of *O. flohri* from Guatemala. Coleopts Bull. 44:211–215.  
Navarrete-Heredia, J. L. and R. Novelo-Gutierrez. 1990. Contributions to the knowledge of

Oxyporinae (Coleoptera: Staphylinidae) associated with mushrooms (Fungi: Basidiomycetes) in Mexico. Coleopts Bull. 44:229–232.

Scheerpeltz, O. 1960. Zur Kenntnis neotropischer Staphyliniden (Col.). Btr. Z. Neotrop. Fauna 2:65–138.

Received 9 November 1990; accepted 16 August 1991.

REVIEW OF THE SPECIES OF *TELEPHANUS* ERICHSON  
FROM THE MALAGASY REGION, WITH  
DESCRIPTION OF A NEW SPECIES  
(COLEOPTERA: SILVANIDAE)

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*Abstract.*—Six species of *Telephanus* Erichson are recorded from the Malagasy Region, including one new species, *Telephanus gomyi*, from Réunion Island. *Telephanus spinosus* Schaufuss is considered a junior synonym and junior homonym of *Telephanus spinosus* Grouvelle. A key to the species and illustrations of the adults are provided and the affinities of this group of species are briefly discussed.

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While examining a collection of Cucujidae (sens. lat.) from the Mascarene Islands (Réunion and Mauritius) in the Muséum d'Histoire Naturelle, Geneva I discovered three specimens of an apparently undescribed apterous, microphthalmic species of *Telephanus*. This led to an examination of the types and other specimens of all five species described from the Malagasy Region (Madagascar and the Mascarene Islands). This study revealed three distinctive groups of species and raised questions over the generic placement of the Old World members of *Telephanus*.

Of about 100 described species of *Telephanus*, Hetschko (1930) listed only eight from the Old World, five from the Malagasy Region and three from southeastern Asia. The remainder are confined to the New World. Adults of *Telephanus* are recognized by the combination of the following character states: securiform maxillary palpi; elongate antennal scapes, frons without longitudinal grooves; closed procoxal cavities; tarsomeres II–III simply lobed; prothorax and often elytra laterally spinose; aedeagus inverted, parameres on ventral aspect of median lobe.

Three species, *Telephanus antennatus* Waterhouse, described from Dory, New Guinea; *T. pictus* Waterhouse, described from Borneo; and *T. spinicollis* Waterhouse, described from Aru, Indonesia, were transferred from *Telephanus* to *Psammoecus* Latreille by Nevermann (1931:198). I have examined the type specimens, housed in the British Museum (Natural History), of those species and agree with Nevermann's conclusion as to their assignment.

It also seems unlikely that the Malagasy members of *Telephanus* are strictly congeneric with the New World members of the genus. The Réunion and Mauritius species share some similarities, especially antennal proportions, with *Indophanus* Pal, a monotypic genus from South India placed near *Psammoecus* and *Telephanus* (Pal, 1981). The four Madagascar species share some character states that are closer to *Uleiota* Latreille than to New World *Telephanus*. These include antennomere III more than twice as long as II and possession of a longitudinally raised lateral margin of the frons. In approximately 30 species examined of New World *Telephanus*, antennomere III is no more than 1.5 times the length of II and the frons is not

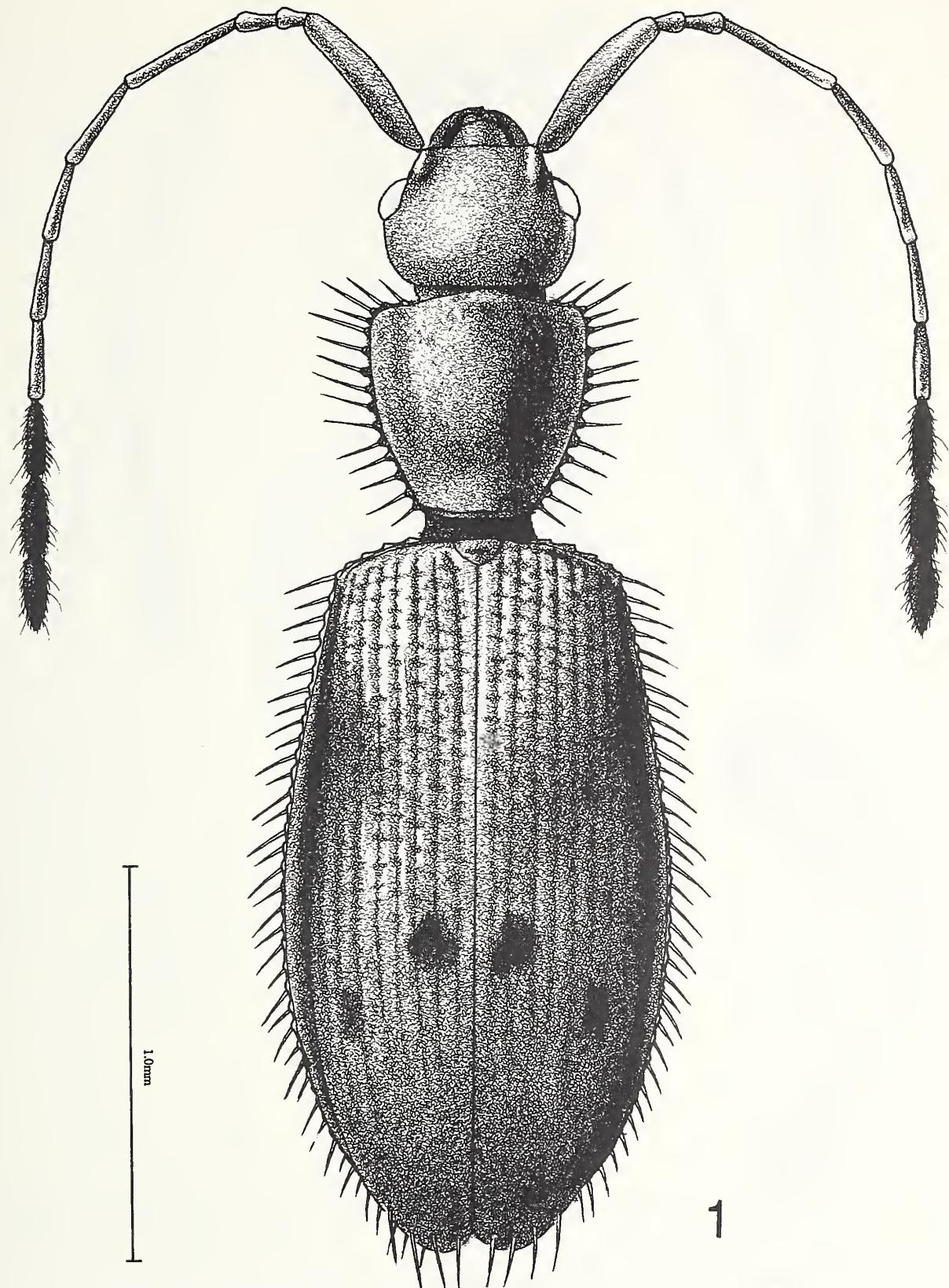


Fig. 1. *Telephanus alluaudi* Grouvelle. Line = 1.0 mm.

laterally margined. The hindwing venation of *T. armatus* (Fig. 14) differs considerably from both *Uleiota dubius* (Fabricius) (Fig. 13) and *Telephanus velox* (Haldemann) (Fig. 15). However, the two species from Mauritius and Réunion resemble New World *Telephanus* in antennal and frontal characters, and it may be that the *Uleiota*-like structures in the Madagascar species represent retention of ancestral character

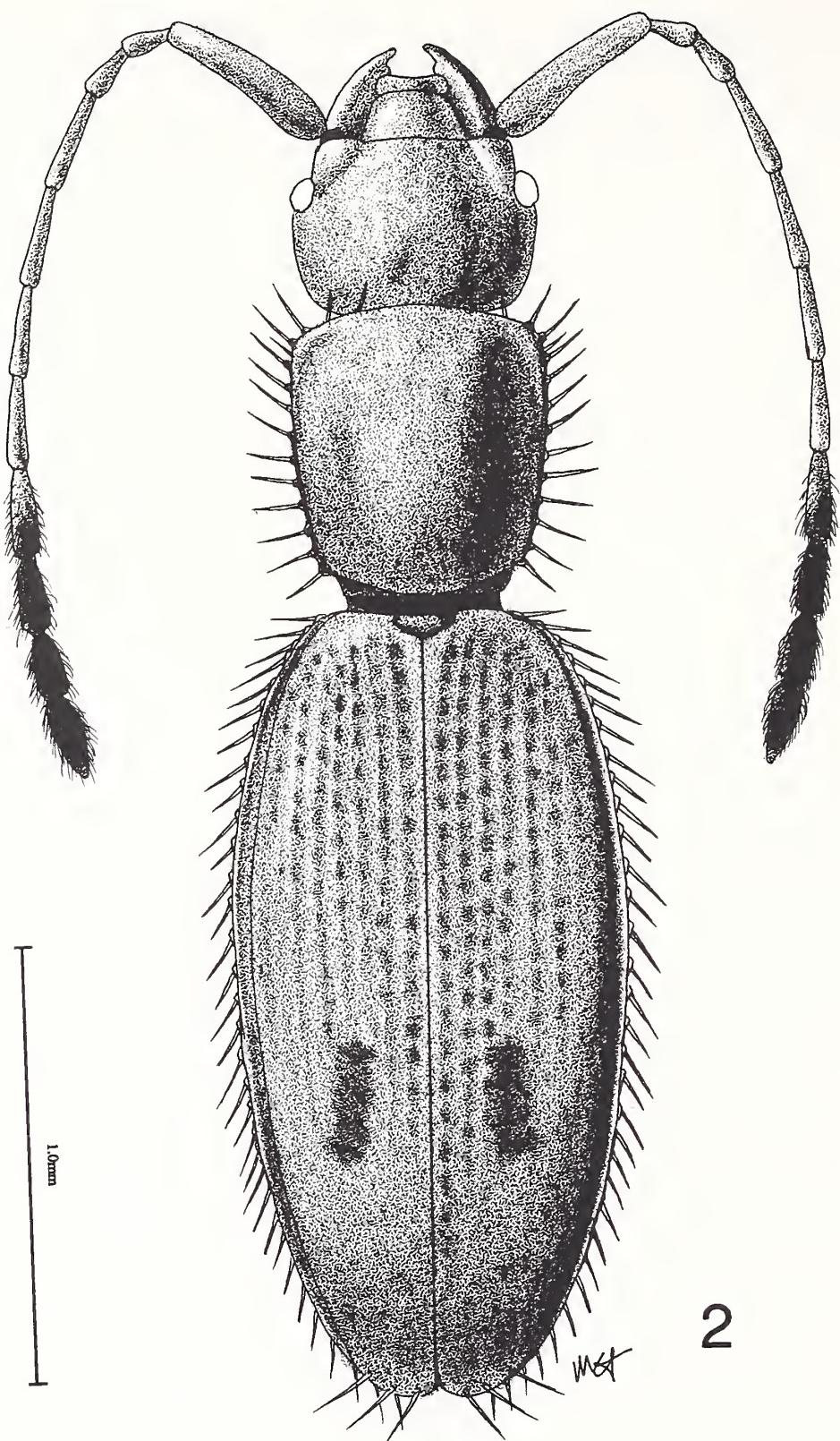


Fig. 2. *Telephanus gomyi*, n. sp. Line = 1.0 mm.

states. For that reason, I am proposing no generic changes at present. The distribution of the species of *Telephanus*, as presently constituted, also is anomalous and suggests that the composition of this genus merits closer study.

The number and disposition of socketed prothoracic spines are important diagnostic features of New World *Telephanus*. Unfortunately, many of the spines are missing from most of the Madagascar specimens examined during this study and

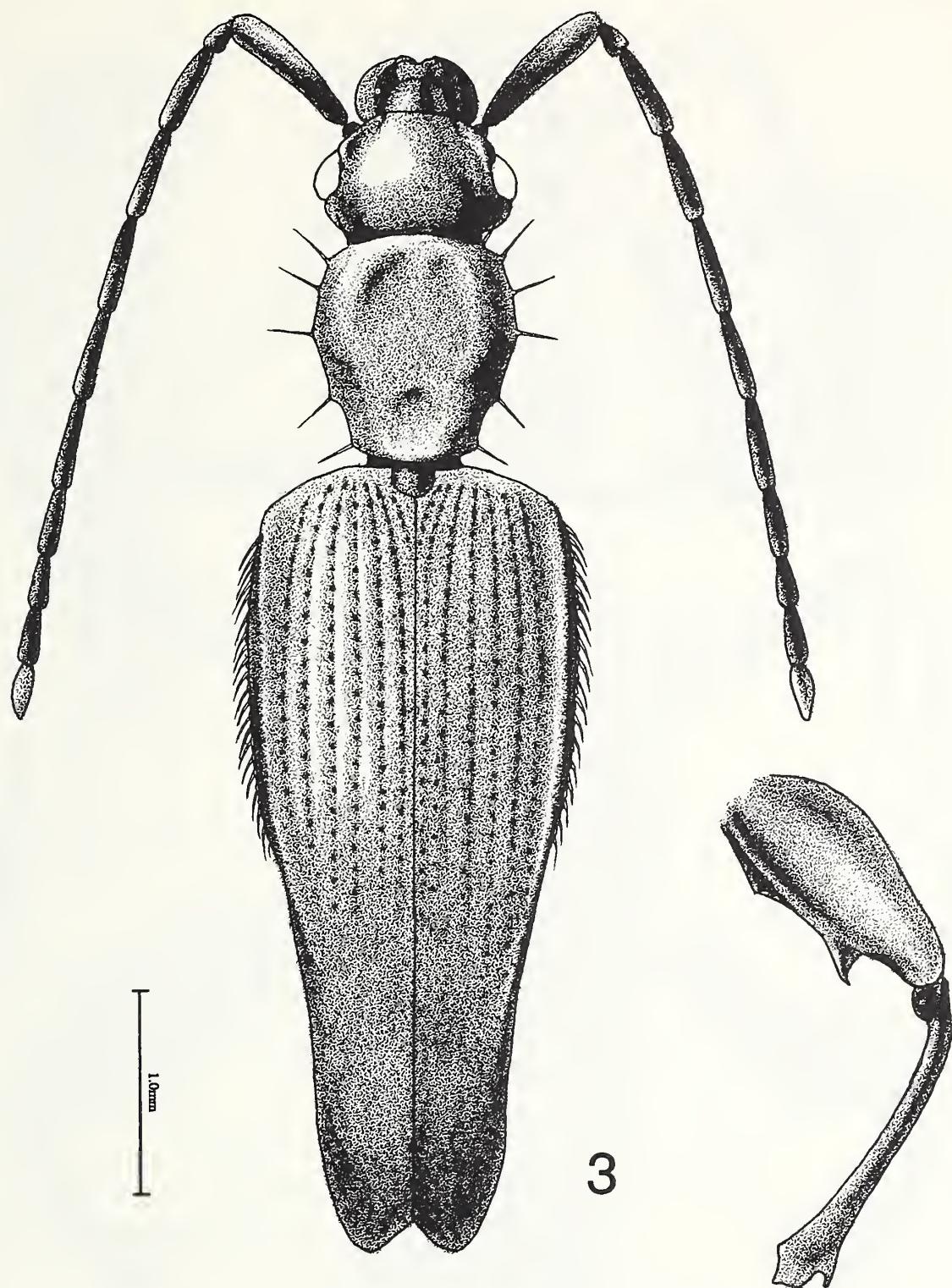


Fig. 3. *Telephanus armatus* Grouvelle, habitus of male. Inset is dorsal view of right hind leg. Line = 1.0 mm.

their presence has been inferred from the empty sockets. The Madagascar specimens examined that bear specific locality information were collected in Antananarivo, spelled either "Annanarivo" or "Antanarivo" on the specimen labels. Members of the type series of three species in the Muséum National d'Histoire Naturelle, Paris were examined by S. A. Slipinski, who affixed lectotype and paralectotype labels to some of the specimens. Since these designations have not been published they are not valid under the International Code of Zoological Nomenclature.

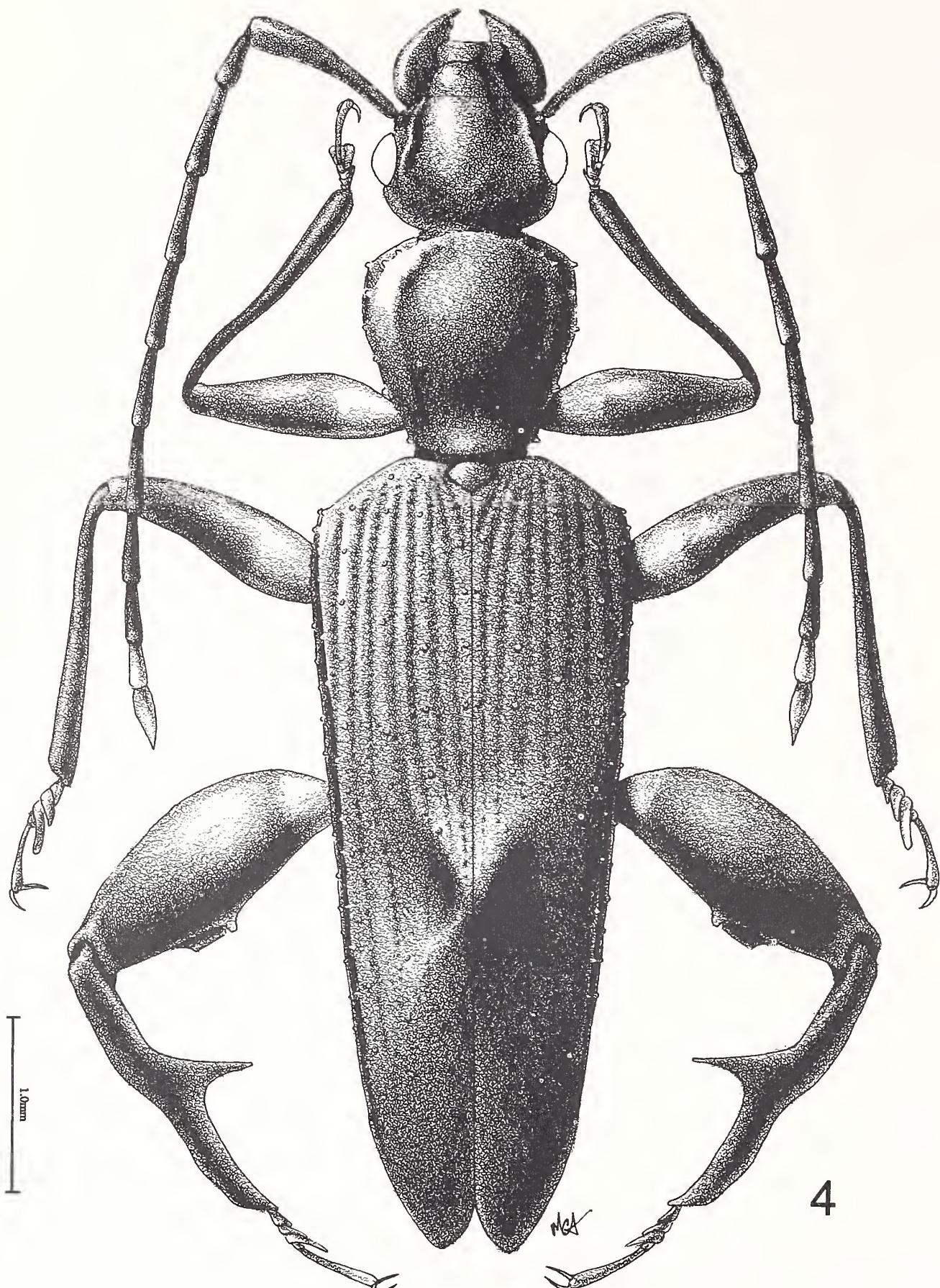
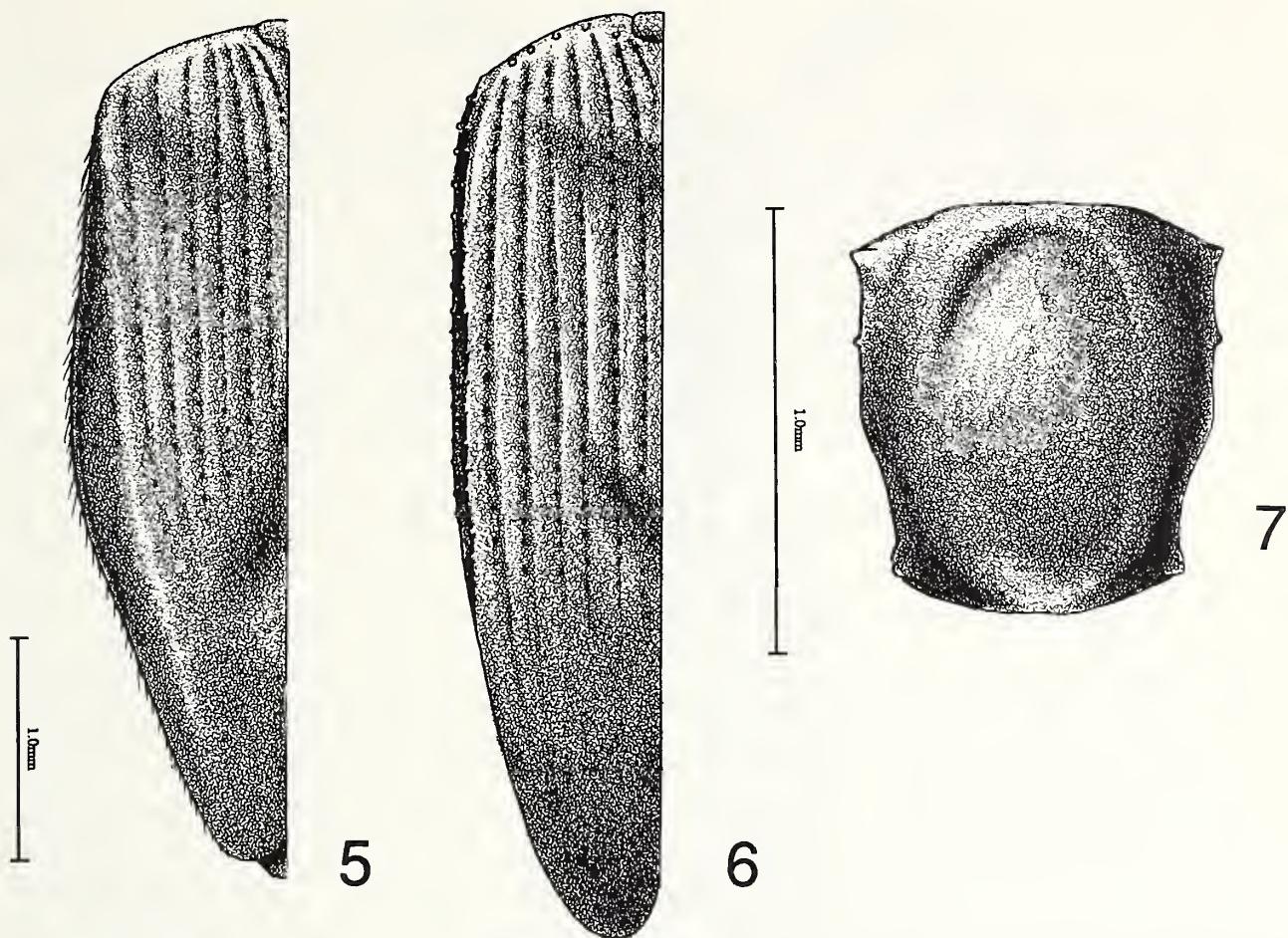


Fig. 4. *Telephanus spinosus* Grouvelle, male. Line = 1.0 mm.



Figs. 5-7. 5. *Telephanus armatus* Grouvelle, left elytron of female. 6. *Telephanus spinosus* Grouvelle, same. 7. *Telephanus cedius* Schaufuss, pronotum. Lines = 1.0 mm.

Specimens were borrowed from the following institutions:

BMNH = British Museum of Natural History, London. Mr. A. D. Kerley.

MCSN = Museo Civico di Storia Naturale "Giacomo Doria," Genova. Dr. Roberto Poggi.

MNHN = Muséum National d'Histoire Naturelle, Paris. Mlle. Nicole Berti.

MHNG = Muséum d'Histoire Naturelle, Geneva. D. Ivan Löbl.

ZMHB = Museum für Naturkunde der Humboldt Universität zu Berlin, Bereich Zoologisches Museum, Berlin. Dr. Fritz Hieke.

#### KEY TO THE SPECIES OF *TELEPHANUS* OF THE MALAGASY REGION

1. Terminal antennomeres dark (Figs. 1, 2). Mascarene Islands ..... 2
- Terminal antennomeres pale (Figs. 3, 4, 8). Madagascar ..... 3
- 2(1). Eyes reduced (Fig. 2), elytral humeri rounded; hind wings absent; median lobe sharply constricted medially, flagellum thick (Fig. 10); Réunion Is ..... *gomyi*, n. sp.
- Eyes not reduced (Fig. 1), elytral humeri normal; hind wings present; median lobe not sharply constricted medially, flagellum slender (Fig. 9); Mauritius ..... *alluaudi* Grouvelle
- 3(1). Elytra paler than head and pronotum ..... 4
- Elytra same color as head and pronotum ..... 5
- 4(3). Pronotum with conspicuous tubercles at antero-lateral angles (Fig. 7) ..... *cedius* Schaufuss

- Pronotum without conspicuous tubercles at antero-lateral angles (Fig. 8) ..... *gracilis* Schaufuss
- 5(3). Trochanter and basal part of femur pale; hind trochanter in male prolonged posteriorly as acute spine (Fig. 12); hind femur in male armed medially with a blunt spine and a carina (Fig. 4), hind tibia armed with a large spine medially on ventral edge; elytral suture in male elevated at about apical third, appearing "pinched"; lateral margin of elytra in female not explanate (Fig. 6) ..... *spinosis* Grouvelle
- Only trochanter pale; hind trochanter in male slightly prolonged posteriorly, truncate; hind femur of male with carina medially and acute spine at about apical third (Fig. 3); hind tibia in male with small tubercle located dorsally near apex (Fig. 3); elytral suture not elevated (Fig. 3); lateral margin of elytra in female explanate (Fig. 5) .. *armatus* Grouvelle

*Telephanus alluaudi* Grouvelle

Figs. 1, 9

*Telephanus Alluaudi* Grouvelle, 1899:172

*Types.* Lectotype, here designated, in MNHN with label data as follows: "I. Maurice Curepipe Ch. Alluaud"/"MUSEUM PARIS 1917 Coll. GROUVELLE"/"Telephanus alluaudi Grouv"/"LECTOTYPE Left sp."/ "PARALECTOTYPE Right"/"Telephanus alluaudi Gru. det S.A. Slipinski 85" [two specimens glued to the same card]. I select the specimen on the left as lectotype and the specimen on the right as paralectotype; 2, "I. Maurice Curepipe Ch. Alluaud 1897"/"TYPE"/"MUSEUM PARIS coll. Alluaud"/"Telephanus alluaudi Grouv" [in Grouvelle's hand] [two specimens glued to same card; both are paralectotypes].

*Type locality.* Described from Curepipe, Mauritius, from an unstated number of specimens.

*Diagnosis.* Adults of this species are most similar to those of the following species, but can be distinguished by their normal humerus (Fig. 1) and metasternum, presence of kind wings, more basally narrowed pronotum (Fig. 1), and structure of the male genitalia (Fig. 9). The elytral maculae (Fig. 1) may be absent. Length 3.0 mm–3.5 mm.

*Biology.* The only information was provided with the original description: "Captured between the leaves of a small species of *Pandanus*."

*Discussion.* This species and the new species described below constitute an easily recognized group within the Malagasy Region components of *Telephanus*, characterized by their small size, coloration, antennal proportions, and male genital structure.

*Telephanus gomyi*, new species

Figs. 2, 10

*Types.* Holotype male in MHNG with data as follows: "La Réunion Cirque de Salazie Piton Marmite 1,800 m. 4-1-1972 Tamisage tronc pourri Y. Gomy." Paratype females, 2, with same data [MHNG].

*Diagnosis.* Most similar to adults of *T. alluaudi*, adults of this species can be distinguished by their small eyes, lack of hind wings and consequent reduction of the humerus and metasternum, more parallel-sided pronotum (Fig. 2) and structure of the male genitalia (Fig. 10).

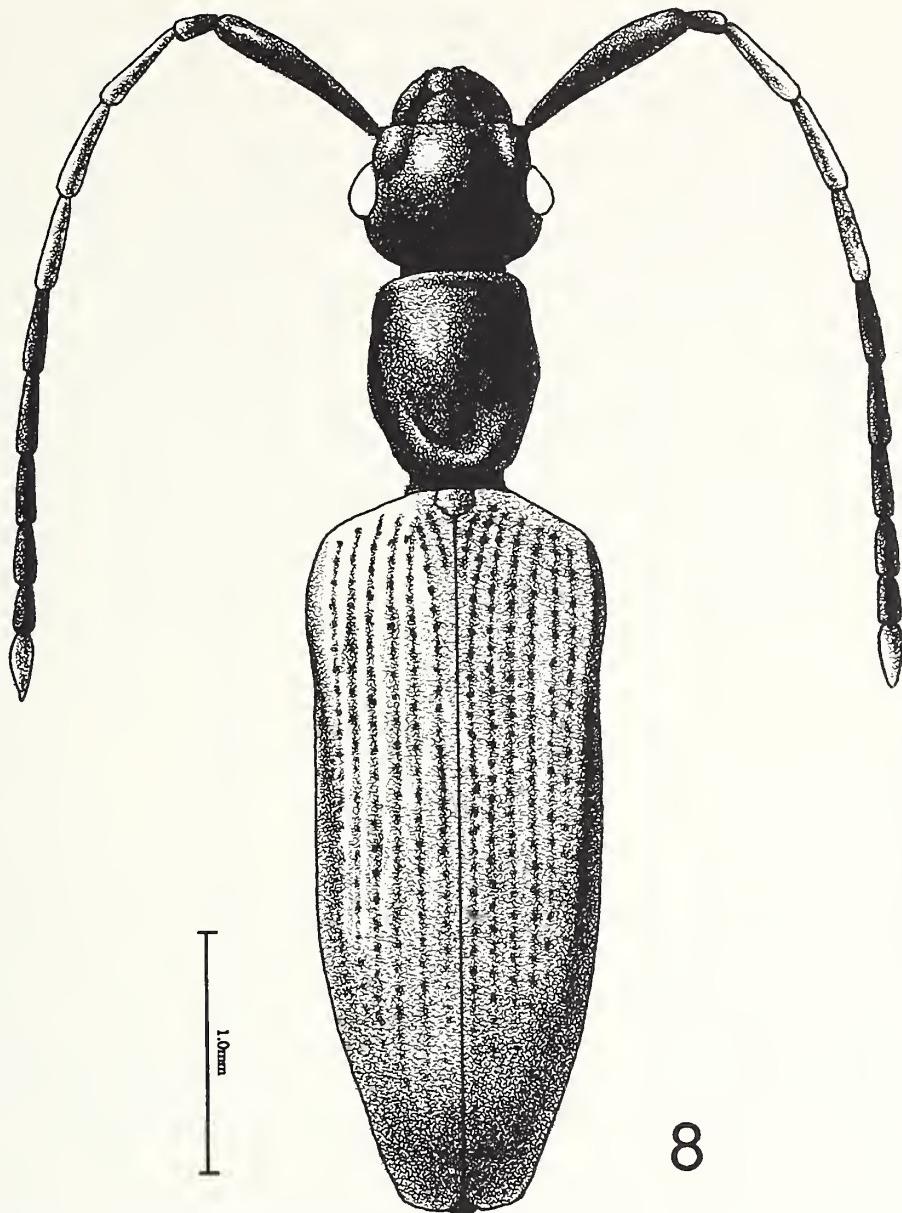
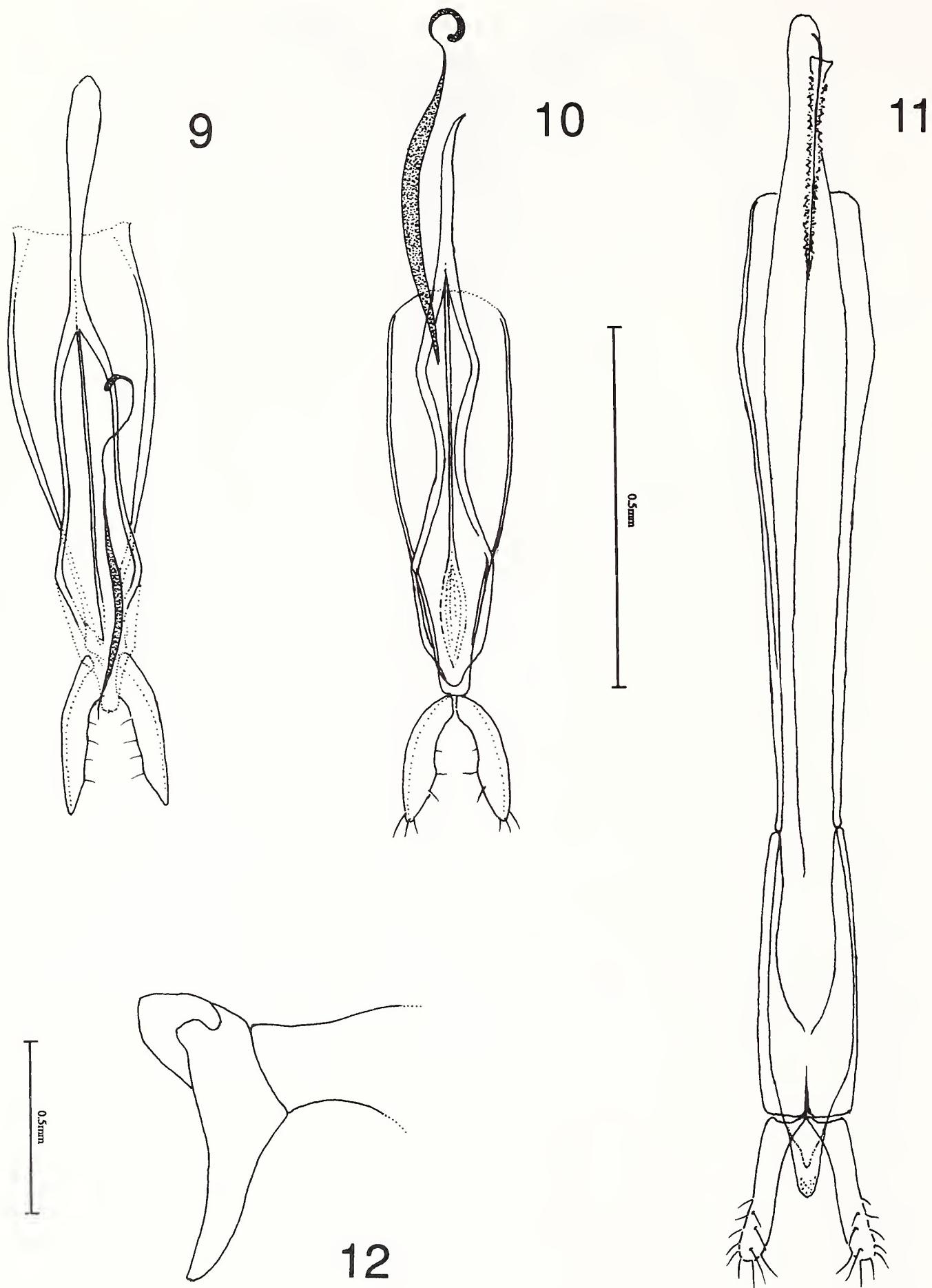


Fig. 8. *Telephanus gracilis* Schaufuss. Line = 1.0 mm.

**Description.** Elongate, narrow. Pale testaceus, appendages somewhat paler, dark markings as follows: antennomeres IX–XI and apex of VIII, elytral maculae at about apical third. Length 2.8 mm. **Head:** Transverse (1:1.18), broadest just behind eyes. Punctuation absent or obscured by coarse tuberculate microsculpture; pubescence composed of pale, stout, recumbent to suberect setae, directed anteriorly; not obscuring surface. Eyes small, in dorsal view about 5 facets wide, length about 0.18 of head capsule length measured from apex of clypeus to basal transverse groove. Antennae elongate, attaining about midpoint of elytra; scape elongate and stout; antennomere proportions as follows: 5:1:1.25:2.75:2.75:2.5:2.25:2.25:2:2:2.25; antennomeres VIII–XI broader than flagellar portion of antenna. **Thorax:** Pronotum subquadrate, slightly longer than broad (1:0.88); broadest across apical angles, gradually, evenly narrowed basally. Anterior angles right, posterior obtuse. Disk broadly, vaguely longitudinally impressed laterally. Surface sculpture and pubescence as head. Lateral margin, beginning at apical angle, with 11 tubercles armed with spines; two additional tubercles and spines are present on each side of the apical margin and one



Figs. 9–12. 9. *Telephanus alluaudi* Grouvelle, male genitalia. 10. *Telephanus gomyi* Thomas, n. sp., male genitalia. 11, 12. *Telephanus spinosus* Grouvelle. 11. Male genitalia. 12. Male anterior trochanter. Lines = 0.5 mm.

is present on each side below and between the 1st and 2nd tubercles. Elytra somewhat oval in shape (length/width 1:0.48), depressed across basal third, humeral angle absent; lateral margin explanate and with spined tubercles; spines alternating slightly in length; striae composed of large, very shallow punctures; pubescence composed of stout, pale setae; rows of setae alternate suberect and directed posteriorly with recumbent and directed laterally; a few much longer setae near apex. *Male genitalia*: Similar to that of *T. alluaudi*, differing in the more constricted median lobe, less apically acute parameres, and broader flagellum (Fig. 10).

*Variation.* There are no obvious sexual differences. The two female paratypes are 2.8 mm and 3.0 mm in length. One has immaculate elytra.

*Discussion.* There are only two other known apterous species of *Telephanus*: *T. darlingtoni* Nevermann (1937) and *T. acrolophus* Thomas (1984), both from the mountains of eastern Jamaica. There do not seem to be any special affinities between the two Jamaican species and *T. gomyi*. This species is named after its collector, Ives Gomy, who collected many rare silvanids and cucujids on Réunion and Mauritius islands.

*Telephanus armatus* Grouvelle  
Figs. 3, 5, 14

*Telephanus armatus* Grouvelle, 1890:127

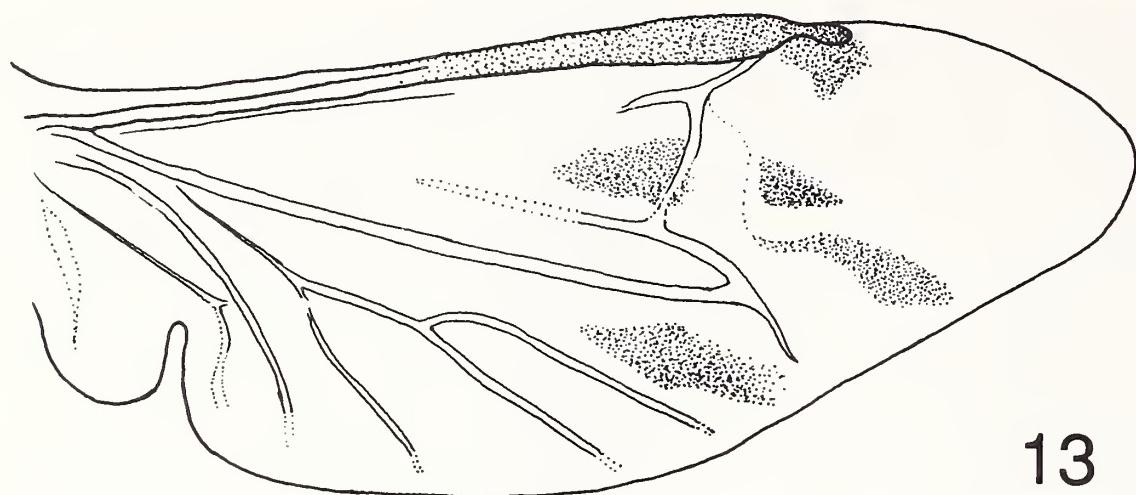
*Types.* Lectotype, here designated, in MNHN with data as follows: "Madagas."/ "exemplaire typique"/"LECTOTYPE"/"MUSEUM PARIS 1917 Coll. GROUVELLE"/"T. armatus A. Grouv"/"Telephanus armatus Grouv det. S.A. Slipinski 85". Paralectotypes, 7, with label data as follows: 1, "Madagas."/ "exemplaire typique"/"MUSEUM PARIS 1917 Coll. GROUVELL"/"PARALECTOTYPE"; 1, "Antananarivo 1889 Sikora"/"Telephanus armatus Grouv. (An. M. C. xxix)"/"Museo Civico di Genova"; 5, "Antananarivo 1889 Sikora"/"Museo Civico di Genova" [MNHN, MCSN]. Although specimens from the type series are housed both in Paris and Genova, Grouvelle's "exemplaire typique" labels on the Paris specimens leave little choice in designating a lectotype.

*Type locality.* Madagascar.

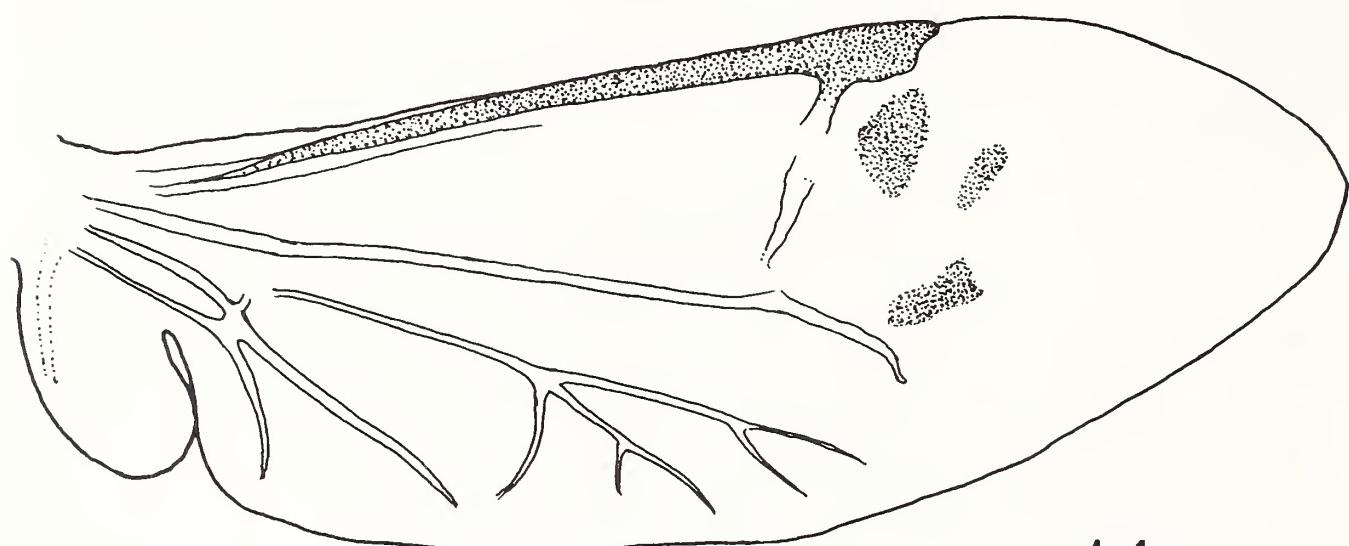
*Diagnosis:* Adults of this species could only be confused with adults of *spinosis*. In both sexes of *armatus* the femora are unicolorous, while the femora are bicolored in both sexes of *spinosis*. Males of both species are easily distinguished by the secondary sexual characters of the hind legs (Figs. 3, 4), and females by the differently shaped elytra (Figs. 5, 6). Length 5.5 mm–6.0 mm.

*Discussion.* The type labels on several specimens listed below are explained by the footnote on the page this species is described (Schaufuss, 1893:598): "While at the printers, Mr. Grouvelle tells me that he has described the species under the above name." For this reason, I do not consider that Schaufuss (1893:598) intended to describe this species as new at the time of publication, and the type labels are spurious. Schaufuss (1893:599) described but did not name a variety in which the last two antennomeres are pale; this is merely individual variation as intermediates occur. Nevermann (1931:198) maintained that the date of Schaufuss' publication was 1890 rather than 1893.

*Distribution.* Madagascar.

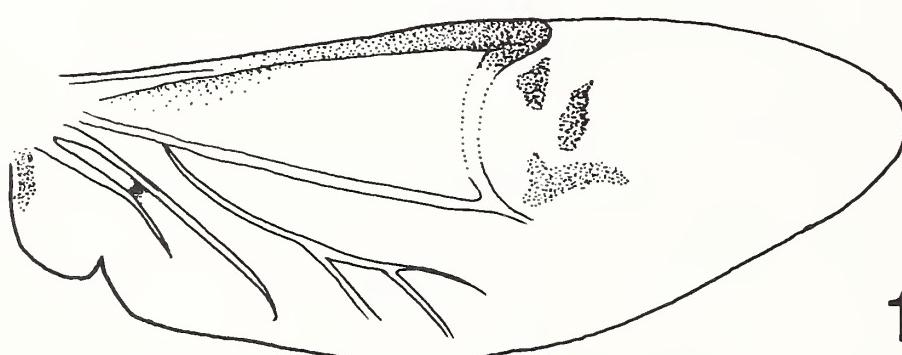


13



14

1.0mm



15

Figs. 13–15. Hind wings. 13. *Uleiota dubius* (Fabricius). 14. *Telephanus armatus* Grouvelle. 15. *Telephanus velox* (Haldeman). Line = 1.0 mm.

*Specimens examined.* 20, as follows: 1, "Type"/"Madagascar"/"Coll. L. W. Schaufuss"/"Telephanus armatus Grouv"/"Zool. Mus. Berlin"; 2, "Coll. L. W. Schaufuss"/"Telephanus armatus var. Type Annanarivo"/"Zool. Mus. Berlin" [both on same pin]; 1, "Type"/"Telephanus armatus var. Type Annanarivo"/"Zool. Mus. Berlin"; 1, "Type"/"Telephanus ar=matus Grouv. Antanarivo"/"Zool. Mus. Berlin"; 7, "Madagascar"/"Zool. Mus. Berlin" [five on one pin, two on a second pin]; 1, "Mad-

agaskar”/“Zool. Mus. Berlin” [there are three specimens on the same pin, two are female *spinosus*, one is a female *armatus*]; 6, “Madagaskar” [one spelled “Madagascar”]/“Zool. Mus. Berlin”; 1, “Madagaskar Antanarivo Sikora S.”/“Telephanus spinosus Gr. det. S. A. Slipinski” [misidentified]. [ZMHB]

*Telephanus spinosus* Grouvelle

Figs. 4, 6, 11, 12

*Telephanus spinosus* Grouvelle, 1890:xcii

*Telephanus spinosus* Schaufuss, 1893:599, NEW SYNONYM, NEW HOMONYM.

**Types.** Of *T. spinosus* Grouvelle, lectotype male, here designated, in MNHN with label data as follows: “Madagascar”/“Type”/“MUSEUM PARIS 1917 Coll. GROUVELLE”/“Telephanus spinosus A. Grouv” [in Grouvelle’s hand]/“LECTOTYPE”/“Telephanus spinosus A. Grou. det S. A. Slipinski 81.” Of *T. spinosus* Schaufuss, lectotype female, here designated, in ZMHB with label data as follows: “Type”/“Telephan. spinosus Schauf. II. [female symbol] Annanarivo”/“Zool. Mus. Berlin.” Three other specimens of the type series are in the ZMHB with data as follows: 1, “Type”/“Telephan. spino=sus Schauf. II. [male symbol] Antanarivo Mag”/“Coll. L. W. Schaufuss”/“Zool. Mus. Berlin” [head and pronotum missing]; 1, “Type”/“Telephan. spino=sus Schauf. II. [female symbol] Antanarivo”/“Coll. L. W. Schaufuss”/“Zool. Mus. Berlin” [pronotum and base of elytra damaged]; 1, “Type”/“Coll. L. W. Schaufuss”/“Telephan, spin-sus Schauf. II. [male symbol] Annanarivo Mag”/“Zool. Mus. Berlin” [fragments only].

**Type locality.** Madagascar.

**Diagnosis.** See diagnosis of *armatus*, above. Length 6.0 mm–6.9 mm.

**Discussion.** Schaufuss (1893:599) clearly felt he was describing this as a new species, preceding his description with: “Teleph. spinosus nov. spec,” even though it had been described by Grouvelle (1890:xcii) three years earlier. Schaufuss (1893:600) noted that he had received specimens of this species from Grouvelle. Hetschko (1930) made no mention of this situation in his catalog.

**Specimens examined:** 6, as follows: 2, “Madagascar”/“Zool. Mus. Berlin” [three cards on pin, one specimen missing]; 1, “Madagascar”/“Zool. Mus. Berlin”; 1, “Madagaskar”/“Telephanus spinosus A. Grouv”/“Zool. Mus. Berlin”; 2, “Madagaskar”/“Zool. Mus. Berlin” [there are three specimens on the same pin, two are female *spinosus*, one is a female *armatus*]. [ZMHB]

*Telephanus cedius* Schaufuss

Fig. 7

*Telephanus cedius* Schaufuss, 1893:601

**Type.** Holotype, in ZMHB with label data as follows: “Telephanus cedius m Type Annanarivo”/“Coll. L. W. Schaufuss”/“Zool. Mus. Berlin”. Head missing, sex unknown.

**Type locality.** Antananarivo, Madagascar.

**Diagnosis.** In addition to the key character mentioned above, in the only known specimen of this species the punctuation of the pronotum is coarser and the micro-sculpture more pronounced than in any of the specimens of *gracilis* examined. Un-

fortunately, the head of the holotype is missing. Schaufuss (1893:601) stated that the antennae of *gracilis* and *cedius* were similar. Schaufuss (1893:601) gave the length of the holotype as 5 mm.

*Telephanus gracilis* Schaufuss

Fig. 8

*Telephanus gracilis* Schaufuss, 1893:600

*Types.* Lectotype, here designated, in ZMHB with following data: "Telephanus gracilis m. Annanarivo Type"/"Coll. L. W. Schaufuss"/"Zool. Mus. Berlin." Sex unknown. Paralectotypes, 6, with label data as follows: 1, "Type"/"Telephanus gracilis m. var. Type Annanarivo"/"Zool. Mus. Berlin"; 1, "Type"/"Telephanus gracilis Schauf. II. Annanariva M."/ "Zool. Mus. Berlin" [damaged]; 4, "Coll. L. W. Schaufuss"/"Zool. Mus. Berlin." [ZMHB]

*Type locality.* Antananarivo, Madagascar.

*Diagnosis.* Individuals of this species are superficially similar to *cedius* in sharing, according to Schaufuss (1893:601), tricolored antennae. They can be distinguished from those of *cedius* by their lack of prominent tubercles on the anterolateral angles of the pronotum (Fig. 8) and the somewhat sparser pronotal macro- and micro-sculpture. Length 4.6 mm–5.0 mm.

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## HYDROPTILIDAE (TRICHOPTERA) OF COSTA RICA: THE GENUS *OXYETHIRA* EATON

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**Abstract.**—Nine new species of *Oxyethira* (Trichoptera: Hydroptilidae) are described from Costa Rica: *O. apinolada*, *O. cuernuda*, *O. culebra*, *O. espinada*, *O. hilosa*, *O. rareza*, *O. sencilla*, *O. sierruca*, and *O. tica*. Males of each new species are described and figured. In addition, distribution records are presented for eight previously described species occurring in Costa Rica: *O. arizona* Ross, *O. azteca* (Mosely), *O. costaricensis* Kelley, *O. glasa* (Ross), *O. janella* Denning, *O. parazteca* Kelley, *O. parce* (Edwards and Arnold), and *O. simulatrix* Flint. A key is provided to males of the Costa Rican species.

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This paper on the genus *Oxyethira* Eaton is the latest addition to our series dealing with the taxonomy and systematics of the microcaddisflies of Costa Rica (Trichoptera: Hydroptilidae). In this paper, we describe nine new species of *Oxyethira* from Costa Rica (one is also known from Panama) and provide distribution records for an additional eight Costa Rican species. These new species and new records are the result of an ongoing field inventory of Costa Rican microcaddisfly biodiversity (Harris and Holzenthal, 1990).

Kelley (1984) provided the most recent review of the genus, its subgenera and species groups, and he included a detailed discussion of male and female morphology. His checklist of the world species included 43 from the Neotropics. The occurrence of 17 species, including nine new species, in Costa Rica alone, suggests that many more Neotropical *Oxyethira* await discovery. Important papers describing portions of the Neotropical *Oxyethira* fauna include those of Botosaneanu (1979) and Flint 1964, 1968a, b) for the Antilles, Mosely (1937) for Mexico, Mosely (1939) for Brazil, Flint (1974) for Surinam, Flint (1980) for Argentina, and Kelley (1983) for the Neotropics in general. Previously described Neotropical *Oxyethira* and their general distribution include *aculea* Ross 1941 (Mexico), *alaluz* Botosaneanu 1979 (Cuba), *andina* Kelley 1983 (S Andes), *arctodactyla* Kelley 1983 (Venezuela), *argentinensis* Flint 1982 (Argentina), *arizona* Ross 1948 (SW USA; Central America; Greater Antilles) (*cirrifera* Flint 1964 is a synonym), *azteca* (Mosely) 1937 (SW USA to Argentina<sup>1</sup>), *bicornuta* Kelley 1983 (N Brazil), *bidentata* (Mosely) 1934 (S Andes), *brasiliensis* Kelley 1983 (Brazil), *campesina* Botosaneanu 1977 (Cuba), *circaverna* Kelley 1983 (Ecuador; Panama), *colombiensis* Kelley 1983 (Colombia), *costaricensis* Kelley 1983 (Costa Rica), *dactylonedys* Kelley 1983 (Paraguay), *dalmeria* (Mosely) 1937 (Mexico), *discaelata* Kelley 1983 (N Brazil), *glasa* (Ross) 1941 (Cuba; SE USA), *hyalina* Müller 1879 (Brazil), *jamaicensis* Flint 1968 (Jamaica), *janella* Denning 1948 (SE USA to Amazon<sup>1</sup>), (*neglecta* Flint 1964 is a synonym), *lagunita* Flint 1981 (N Argentina to S Brazil), *longissima* Flint 1974 (Surinam), *macrosterna* Flint 1974

(Surinam; N Brazil), *maryae* Kelley 1983 (Colombia), *maya* Denning 1947 (SE USA; Mexico), *merga* Kelley 1983 (Venezuela), *obscura* Flint 1974 (Surinam), *parazteca* Kelley 1983 (Costa Rica; Ecuador), *parce* (Edwards and Arnold) 1961 (SW USA to Peru<sup>1</sup>), *paritentacula* Kelley 1983 (Belize), *puertoricensis* Flint 1968 (Puerto Rico), *quelinda* (Botosaneanu) 1979 (Cuba), *quinquaginta* Kelley 1983 (Ecuador), *santiagensis* Flint 1982 (N Argentina to S Brazil), *scaeodactyla* Kelley 1983 (Ecuador), *simulatrix* Flint 1968 (Jamaica; Central America), *spirogyrae* Müller 1879 (Brazil), *spissa* Kelley 1983 (Brazil), *tega* Flint 1968 (Cuba; Jamaica), *ulmeri* Mosely 1937 (SW USA; N Mexico), *unispina* Flint 1974 (Surinam), *vipera* Kelley 1983 (S Andes), *zilaba* (Mosely) 1939 (Brazil; Paraguay; Argentina). Complete citations of papers containing original descriptions of these species can be found in Kelley's (1984) paper.

Terminology for this paper follows that of Marshall (1979). In Figures 1–9, letters A, B, and C refer to lateral, dorsal, and ventral views, respectively, of the genitalia; E and F are lateral and dorsal (or ventral where indicated) views of the phallus or internal sclerites of the female genitalia. Type material will be deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH), the Instituto Nacional de Biodiversidad, Costa Rica (INBIO), the University of Minnesota Insect Collection, St. Paul (UMSP), and the University of Alabama, Tuscaloosa (UAL), as indicated below. All specimens of previously described species upon which new records are based are from UMSP, except where indicated.

### *Oxyethira* Eaton

*Oxyethira* Eaton, 1873:143. Type species by original designation, *Hydroptila costalis* Curtis, is a species of *Orthotrichia* and should be replaced by *Hydroptila flavigornis* Pictet, according to Neboiss 1963.

Adult *Oxyethira* can be recognized by the presence of three ocelli, a 0-3-4 tibial spur formula, and a mesoscutellum with its anterior margin convex and its posterior margins slightly concave. General characteristics of the male genitalia include sternum VII with a short, apicomesal process; tergum and sternum VIII excised apically; segment IX withdrawn into segment VIII, with upper half often reduced to a transverse band and venter pointed or broadly rounded anteriorly; segment X membranous and indistinct; the presence of a subgenital plate with a bilobed process originating at its basoventral margin; and a pair of short, fused inferior appendages. The phallus is typically long and slender with a variety of modifications including sclerotized processes, spines, and membranous lobes.

Characteristics of the female genitalia include sternum VII with a short process; reduction of segments VIII, IX, and X; segment VIII narrowed laterally into anteriorly directed apodemes, and X terminating in a pair of cerci. Several internal processes and sclerites associated with the reproductive structures are diagnostic in the females. These include the spermathecal process, which originates anteroventrally, and the associated spermathecal sclerite; the sclerotized dorsum of the oviduct; the posterior

<sup>1</sup> The discovery of *O. tica* and the resurrection of *O. parce* from synonymy with *O. azteca* requires a reassessment of the distributions of these species.

ring sclerite which encircles the oviduct in some species; and in species of the Azteca Group a pair of ventral processes which support the oviduct.

Wiggins (1977) provided a detailed description of the fifth instar larva of the genus. Larvae typically live in standing water or the slower areas of rivers. Fifth instar larvae build transparent, flattened, bottle-shaped cases entirely of silk. Larvae generally feed by puncturing filamentous algal cells and sucking out the cytoplasm.

### Oxyethira apinolada, new species

Fig. 1

This species appears to be a member of Kelley's (1984) Aeola Group of the subgenus *Oxytrichia*. It is somewhat similar to *O. viperina* Kelley in the dorsolateral projections of segment IX and the dorsolateral incision of segment VIII, although this incision is much shorter in the new species. It differs from *O. viperina* in the longer inferior appendages, trilobed subgenital plate, and absence of bilobed processes.

*Male.* Length 2.4–2.6 mm. Brown in alcohol. Antennae with 27 segments. Genitalia as in Figure 1. Abdominal sternum VII with short, apicomesal process. Segment VIII with lightly sclerotized, setose, dorsolateral lobes; tergum VIII with broad, shallow, mesal excavation; sternum VIII with deep, V-shaped, mesal excavation. Segment IX extending anteriorly to middle of segment VII; in dorsal view, posterior portion wide and rounded; in lateral view, posterior portion narrow, tapered; segment IX bearing elongate, narrow, apically acute, sclerotized, dorsolateral processes. Segment X membranous, indistinct. Inferior appendages sclerotized, elongate, slightly convex in lateral view; tapering to acute apex; in ventral view, rectangular. Subgenital plate tapering posteriorly; in ventral view, wide, trilobed, the lateral lobes bearing numerous stout setae. Bilobed processes absent. Phallus somewhat rectangular; bearing sclerotized subapical process nearly encircling distal membranous lobe and second, short, acute, subapical, sclerotized process.

*Holotype.* Male, COSTA RICA: GUANACASTE: Parque Nacional Rincón de la Vieja, Quebrada Agua Apinolada, 10.759°N, 85.292°W, el. 795 m, 25.vi.1986, Holzenthal, Heyn, Armitage (NMNH).

*Paratype.* COSTA RICA: ALAJUELA: Río Pizote, 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth, 1 male (UMSP).

*Etymology.* Named for the type locality, Quebrada Agua Apinolada.

### Oxyethira cuernuda, new species

Fig. 2

This species appears to be a member of subgenus *Tanytrichia* Kelley based on the elongate nature of segment IX and general structure of the phallus. The elongate dorsal processes of segment VIII and the bifid lateral processes of the phallus separate the new species from others in the subgenus.

*Male.* Length 2.0–2.4 mm. Brown in alcohol. Antennae with 26 segments. Genitalia as in Figure 2. Abdominal sternum VII with short, apicomesal process. Segment VIII with dorsolateral margin produced into a long, thin process; tergum and sternum VIII deeply excised. Segment IX elongate, narrow; extending anteriorly beyond middle of segment VI. Segment X membranous, indistinct. Inferior appendages in lateral view short, sclerotized, acute posteriorly; in ventral view widely separated, apices

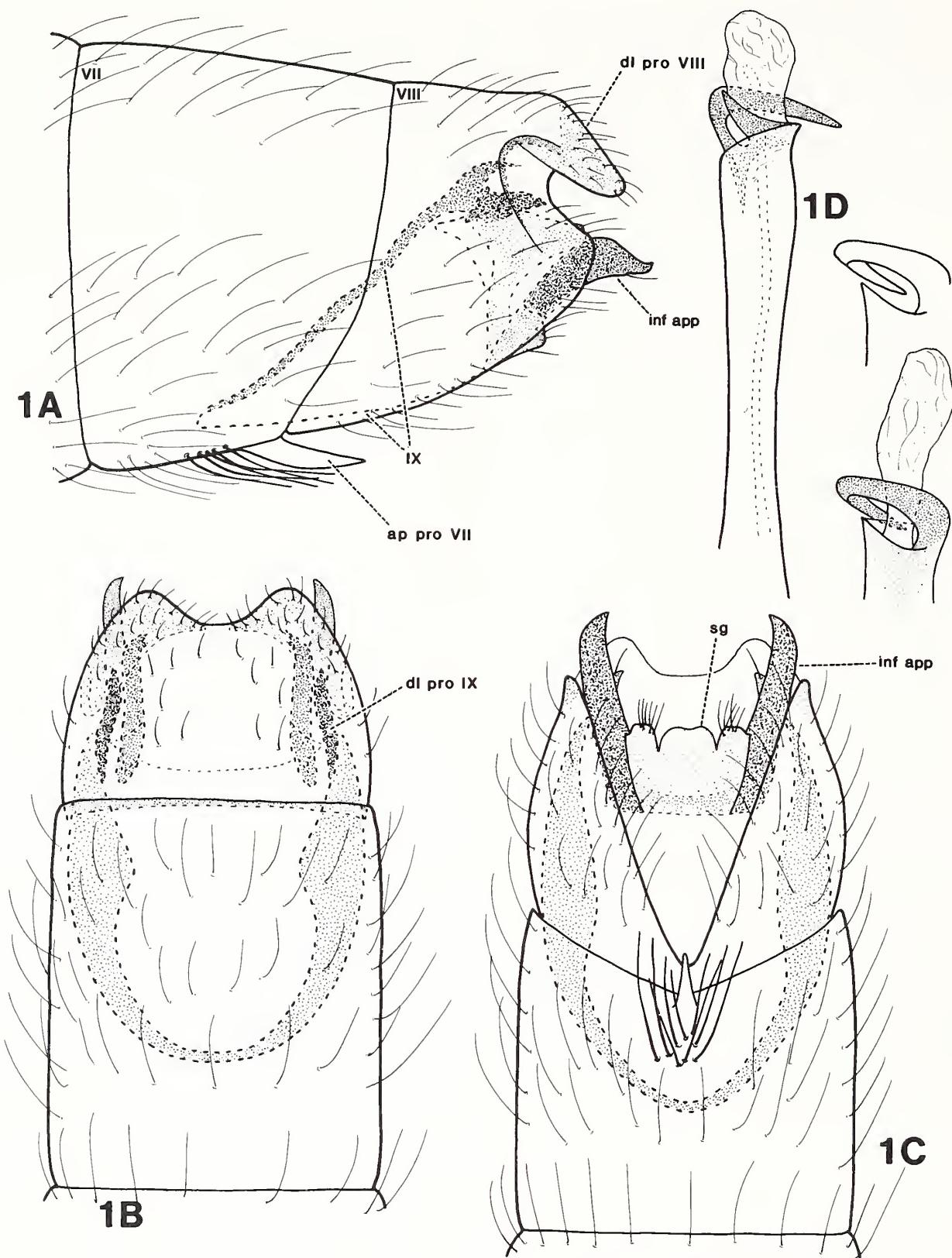


Fig. 1. *Oxyethira apinolada*, new species, male genitalia. A. Lateral. B. Dorsal. C. Ventral. D. Phallus, lateral; inset, details of apical sclerites. Abbreviations: VII, VIII, IX = abdominal segments VII, VIII, IX, respectively; ap pro VII = apicomesal process of segment VII; dl pro IX = dorsolateral process of segment IX; dl pro VIII = dorsolateral process of segment VIII; inf app = inferior appendage; sg = subgenital plate.

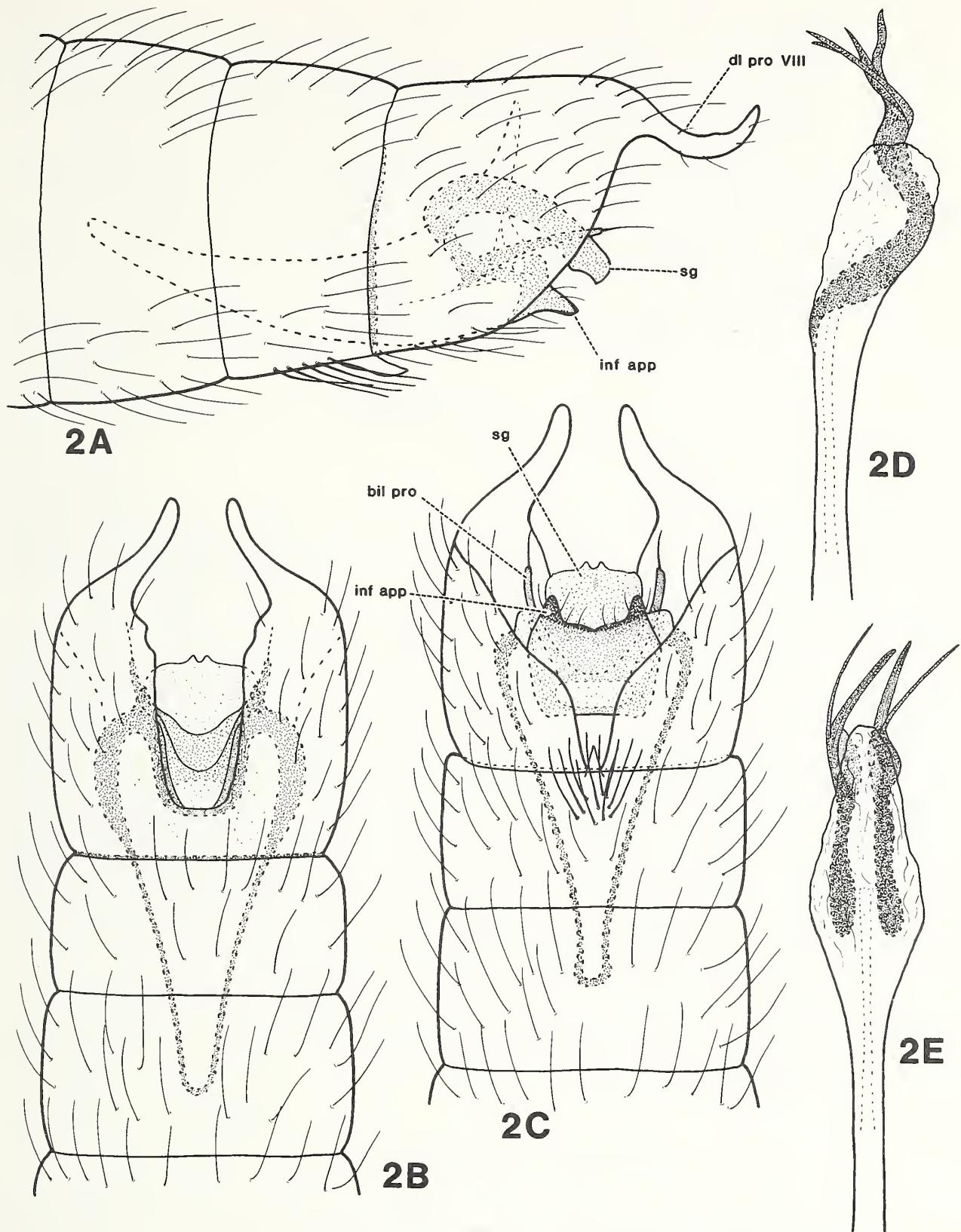


Fig. 2. *Oxyethira cuernuda*, new species, male genitalia. A. Lateral. B. Dorsal. C. Ventral. D. Phallus, lateral. E. Phallus, ventral. Abbreviations: bil pro = bilobed process; others as in Figure 1.

narrow. Subgenital plate in lateral view elongate, narrow, and ventrally curved, apicoventral margin with shallow notch; in ventral view wide, with pair of small mesal projections. Bilobed processes elongate, bearing stout apical setae. Phallus elongate, apex bulbous, membranous, bearing pair of apicolateral sclerites, each divided distally into thin processes.

*Holotype.* Male, COSTA RICA: ALAJUELA: Río Pizote, 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth (NMNH).

*Paratypes.* COSTA RICA: same data as holotype, 26 males (NMNH, UMSP, INBIO, UAL); same, except 5 km N Dos Ríos, 10.948°N, 85.291°W, 9.iii.1986, Holzenthal and Fasth, 9 males (UMSP).

*Etymology.* Spanish: "with horns," referring to the hornlike processes of segment VIII.

#### *Oxyethira culebra*, new species

Fig. 3

*Oxyethira culebra* is a member of the Aeola Group, most similar to *O. bidentata* (Mosely). Both species have elongate, dorsolateral, rodlike processes associated with abdominal segment IX, but *O. culebra* differs from *O. bidentata* and all others in the group in the structure of the inferior appendages.

*Male.* 2.8 mm. Brown in alcohol. Antennae broken. Genitalia as in Figure 3. Abdominal sternum VII with short, apicomesal process. Segment VIII with shallow dorsolateral emargination; tergum VIII with broad, shallow, mesal excavation and rounded lateral lobes; sternum VIII with deep, V-shaped, mesal excavation. Segment IX narrow, extending anteriorly to middle segment VI; bearing narrow, elongate, sinuate dorsolateral processes, each with single, long apical seta. Segment X membranous, apex rounded in dorsal view. Inferior appendages in lateral view elongate, narrow, their apices acute, upturned; each with pair of small subapicoventral lobes; in ventral view, inferior appendages apically divergent, each with subapicomesal sclerotized point and setose lobe. Subgenital plate and bilobed processes absent. Phallus narrow, sinuate; ejaculatory duct protruding from apex, hairlike.

*Holotype.* Male, COSTA RICA: ALAJUELA: Río Pizote, 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth (NMNH).

*Etymology.* Spanish: "snake," referring to the sinuate phallus and dorsolateral processes of segment IX.

#### *Oxyethira espinada*, new species

Fig. 4

This species belongs to the subgenus *Tanytrichia* Kelley and is most closely related to *O. paritentacula* Kelley. It shares with that species the widely separated dorsal processes of abdominal segment VIII. However, in *O. espinada* these processes are short, do not converge apically, and have a series of large, dorsal, apical and subapical spinelike setae.

*Male.* Length 2.5–2.7 mm. Brown in alcohol. Antennae with 34 segments. Genitalia as in Figure 4. Abdominal sternum VII with short, apicomesal process. Segment VIII in lateral view very acute posteriorly, apex upturned; sternum VIII with deep, narrow, U-shaped, mesal excavation; tergum VIII with paired, narrow, sclerotized, dorsobasal

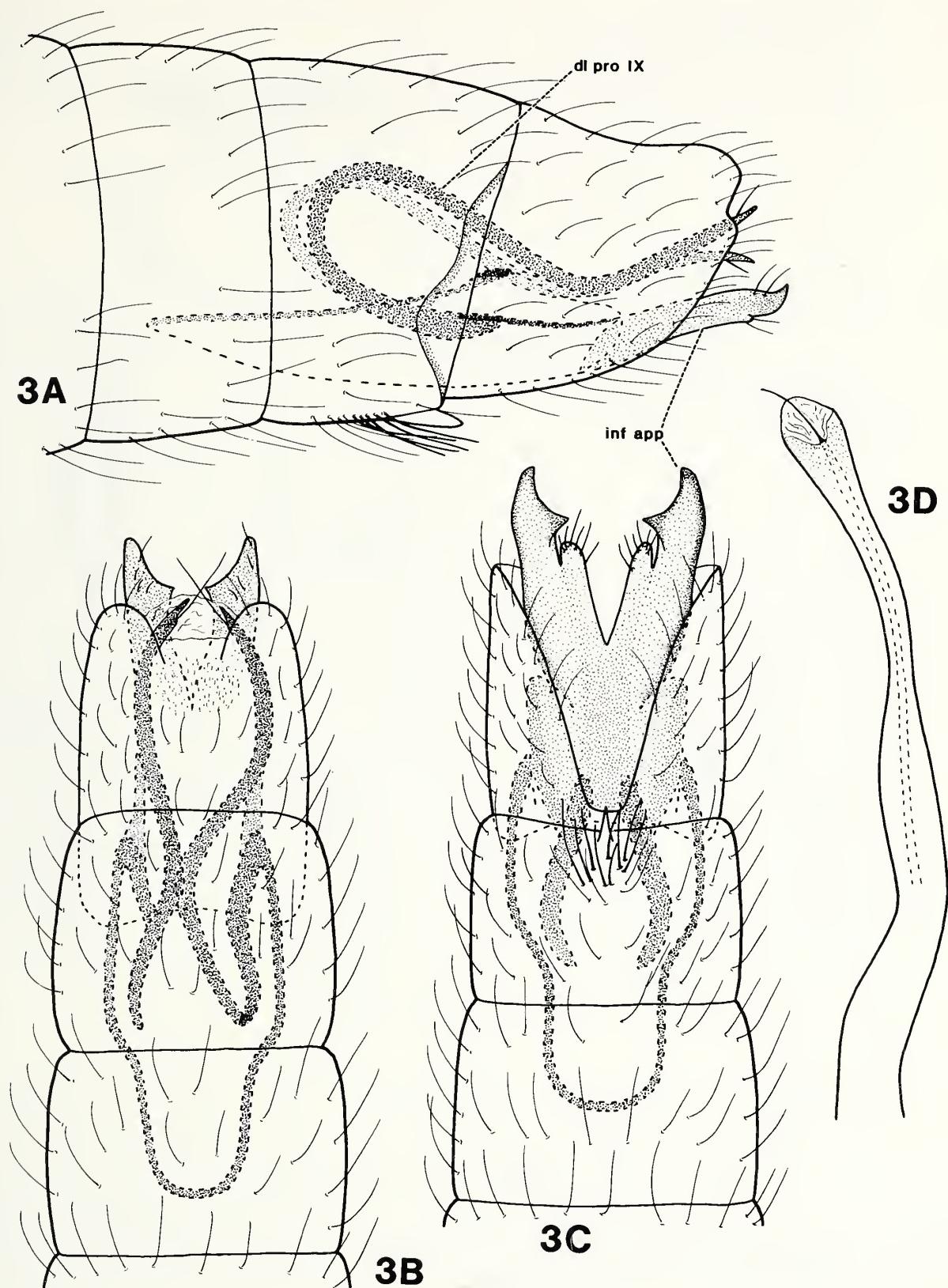


Fig. 3. *Oxyethira culebra*, new species, male genitalia. A. Lateral. B. Dorsal. C. Ventral. D. Phallus, lateral. Abbreviations as in Figures 1 and 2.

processes; each process bearing several stout, apicodorsal and subapicodorsal, spine-like setae. Segment IX elongate, narrow, extending anteriorly to middle of segment VI. Segment X membranous, indistinct. Inferior appendages in lateral view short, apically acute; in ventral view, widely separated, apically truncate. Subgenital plate

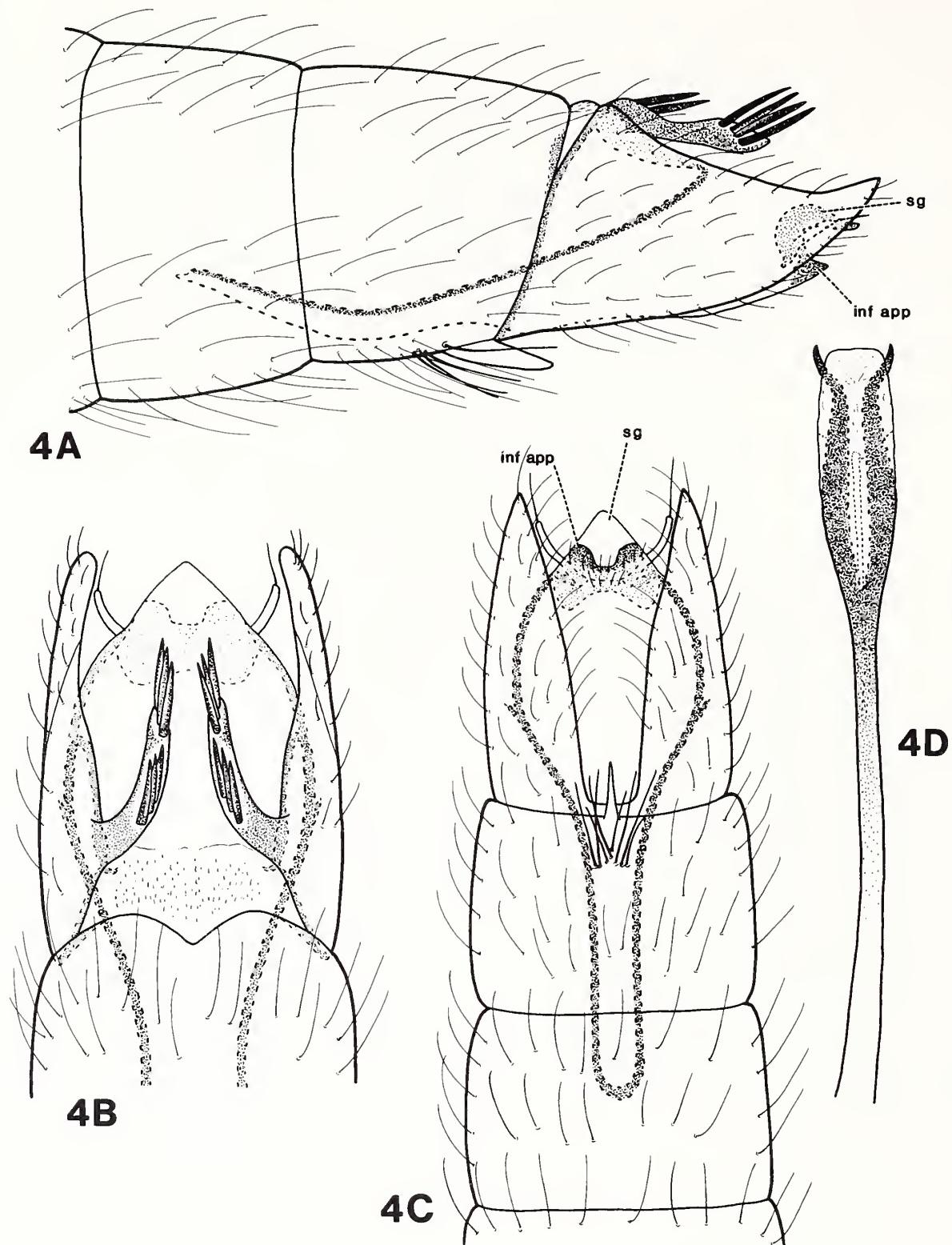


Fig. 4. *Oxyethira espinada*, new species, male genitalia. A. Lateral. B. Dorsal. C. Ventral. D. Phallus, ventral. Abbreviations as in Figures 1 and 2.

in lateral view short, base rounded, apex acute; in ventral view, triangular. Bilobed processes elongate, each bearing stout apical seta. Phallus with basal portion elongate, tubular; distal portion bearing two sclerotized lateral processes, each with acute, outwardly directed apex.

*Holotype.* Male, COSTA RICA: ALAJUELA: Río Pizote, 5 km N Dos Ríos, 10.948°N, 85.291°W, 9.iii.1986, Holzenthal and Fasth (NMNH).

*Paratypes.* Same data as holotype, 2 males (UMSP, UAL); same, except 5 km (air)

S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth, 1 male (INBIO).

*Etymology.* Spanish: “having spines,” referring to the spine-laden dorsal processes of segment VIII.

### Oxyethira hilosa, new species

Fig. 5

In most aspects this species is similar to *O. paritentacula* Kelley (subgenus *Tanytrichia*), but the distinctive phallus of the new species, with its threadlike lateral projections, clearly separates the new species from *O. paritentacula*.

*Male.* Length 1.7–2.2 mm. Brown in alcohol. Antennae broken. Genitalia as in Figure 5. Abdominal sternum VII with short, apicomesal process. Segment VIII in lateral view acute posteriorly; sternum VIII with deep mesal excavation; tergum VIII with paired, sclerotized, basodorsal processes, their bases narrowly separated, their apices narrow, acute, slightly convergent. Segment IX elongate, narrow; extending anteriorly well into segment VI. Segment X membranous; truncate in lateral view, rounded in dorsal view. Inferior appendages short in lateral view, their apices rounded; in ventral view, widely separated with apices slightly triangular. Subgenital plate in lateral view wide; in ventral view wide, with rounded apicomesal protuberance. Bilobed processes elongate, each bearing stout, apical seta. Phallus with pair of long lateral arms arising in mesal membranous area; each arm thin, strongly recurved dorsally, with dorsal, threadlike, subapical extension.

*Holotype.* Male, COSTA RICA: ALAJUELA: Río Pizote, 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth (NMNH).

*Paratypes.* Same data as holotype, 13 males (UMSP, UAL, INBIO); PANAMA: International Canal Zone, Lion Hill, 26.vii.1981, R. B. Kimsey, 3 males (NMNH).

*Etymology.* Spanish: “having threads,” referring to the distinctive phallus.

### Oxyethira rareza, new species

Fig. 6

This species is aberrant within the genus in most respects. It shares in common with *O. quinquaginta* Kelley (*incertae sedis*) vestigial inferior appendages and an asymmetrical subgenital plate, but it also shares similar elongate, dorsal processes of segment IX with *O. andina* Kelley (Aeola Group of subgenus *Oxytrichia*).

*Male.* Length 1.8–2.1 mm. Brown in alcohol. Antennae with 34 segments. Genitalia as in Figure 6. Abdominal sternum VII with broad, V-shaped mesal excavation; lacking apicomesal process. Segment VIII in lateral view acute posteriorly; sternum VIII with very deep, narrow, V-shaped excavation; tergum VIII with broad, U-shaped excavation. Segment IX narrow, extending anteriorly well into segment VI; tergum IX a narrow, sclerotized ribbonlike band extending posteriorly through segment VIII, its apex recurved. Inferior appendages vestigial. Subgenital plate asymmetrical, developed only on left side, its apex bearing long, narrow, sclerotized arm. Left bilobed process long, thin, apex with stout seta; right bilobed process absent. Phallus short, stout, with narrow, subapicolateral sclerotized strip; apex of phallus membranous, ejaculatory duct protruding.

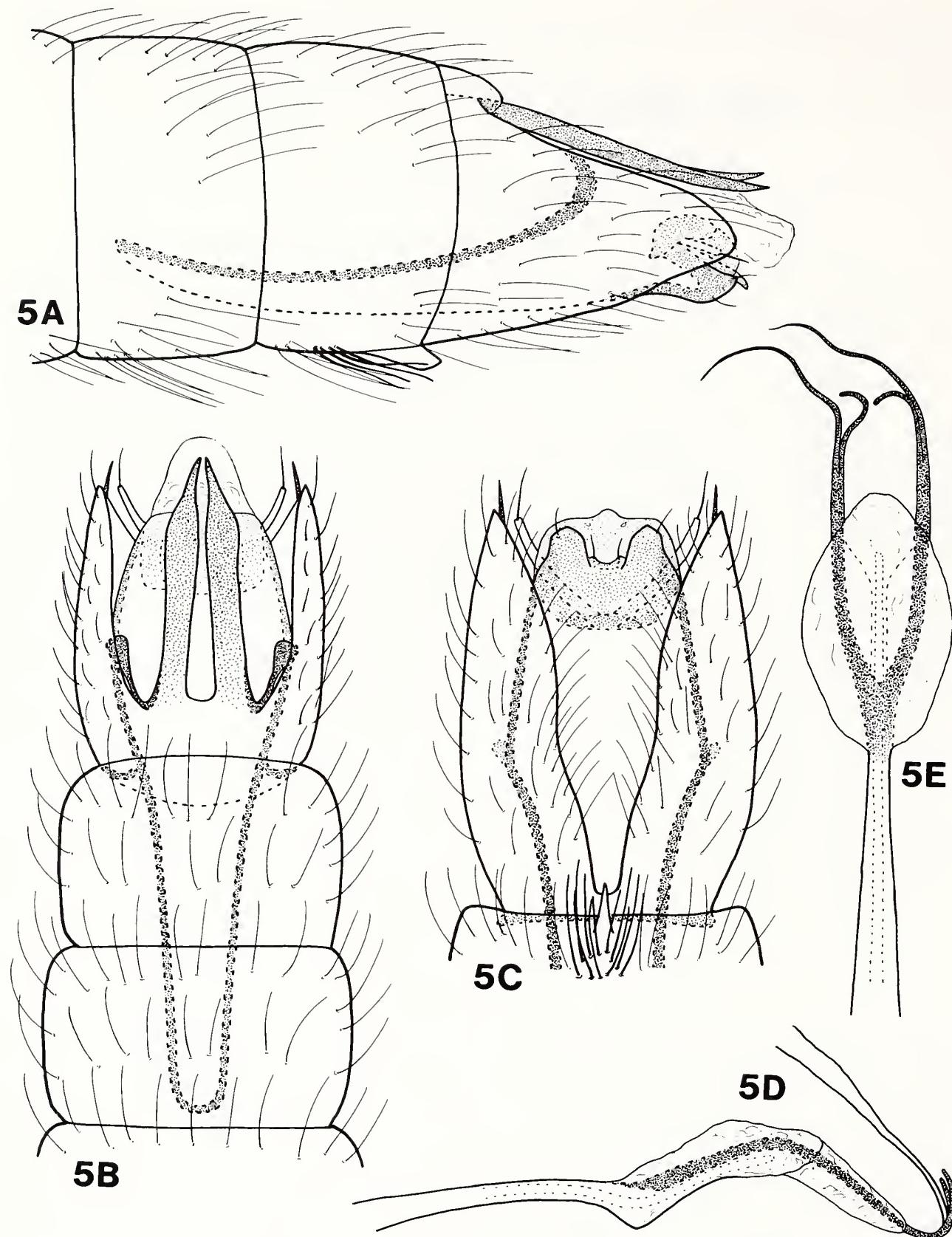


Fig. 5. *Oxyethira hilosa*, new species, male genitalia. A. Lateral. B. Dorsal. C. Ventral. D. Phallus, lateral. E. Phallus, ventral.

**Holotype.** Male, COSTA RICA: ALAJUELA: Río Pizote, 5 km N Dos Ríos, 10.948°N, 85.291°W, el. 470 m, 9.iii.1986, Holzenthal and Fasth (NMNH).

**Paratypes.** Same data as holotype, 1 male (INBIO); same, except 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth, 4 males

(UMSP, UAL); HEREDIA: Quebrada Sura, Est. Biol. La Selva, 10.437°N, 84.010°W, el. 50 m, 20–21.vi.1986, Holzenthal, Heyn, Armitage, 1 male (UMSP).

**Etymology.** Spanish: “oddity,” referring to the unique genitalic structures of this species.

### Oxyethira sencilla, new species

Fig. 7

This new species shares similarities with *O. macrosterna* Flint and related species (subgenus *Tanytrichia*), but can be separated from other species in the subgenus by the absence of the lateral phallic processes in the new species.

**Male.** Length 2.0–2.2 mm. Antennae with 27 segments. Brown in alcohol. Genitalia as in Fig. 7. Abdominal sternum VII with short, apicomosal process. Segment VIII narrow; in lateral view with posterodorsal emarginations; tergum VIII with truncate, mesal excavation and pair of lateral lobes; sternum VIII with deep, U-shaped excavation. Segment IX narrow, tapered, extending anteriorly into segment V. Segment X indistinct, membranous. Inferior appendages short, apices acute; in ventral view widely separated, apices appearing rounded. Subgenital plate in dorsal and ventral views narrow with small apical excision; in lateral view thin, apex narrow. Bilobed processes thin, elongate, each bearing stout apical seta. Phallus short, stout; with pair of sclerotized, distal processes—dorsal one thin, apically acute, median one crescent shaped; phallus when distended truncate distally, with prominent sickle-shaped dor-solateral process.

**Holotype.** Male, COSTA RICA: ALAJUELA: Río Pizote, 5 km N Dos Ríos, 10.948°N, 85.291°W, el. 470 m, 9.iii.1986, Holzenthal and Fasth (NMNH).

**Paratypes.** Same data as holotype, 14 males (UMSP, INBIO); same, except 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth, 2 males (UAL).

**Etymology.** Spanish: “simple, unadorned,” referring to this species’ lack of distinct genitalic structures.

### Oxyethira sierruca, new species

Fig. 8

This species is most similar to *O. quinquaginta* Kelley (*incertae sedis*, according to Kelley, 1984), with which it shares several atypical characters. These include the many antennal segments, the vestigial inferior appendages, and the asymmetrical dorsal arms of the subgenital plate. The new species is distinguished from its congeners by the serrate margin of segment VIII and the structure of the phallus.

**Male.** Length 2.6–3.3 mm. Brown in alcohol. Antennae with 45 segments. Abdominal sternum VII with long apicomosal process. Segment VIII with posterodorsal margin serrate, ragged; sternum VIII extended posteriorly; in ventral view with deep, quadrate excavation and rounded lateral lobes; tergum VIII with small, shallow, rounded excavation. Segment IX narrow in lateral view, rounded anteriorly in dorsal and ventral views; extending anteriorly into segment VII; tergum IX reduced to thin band. Inferior appendages vestigial. Subgenital plate reduced to rounded mesal lobe, but with pair of prominent, asymmetrical dorsal arms—left arm with wide apex

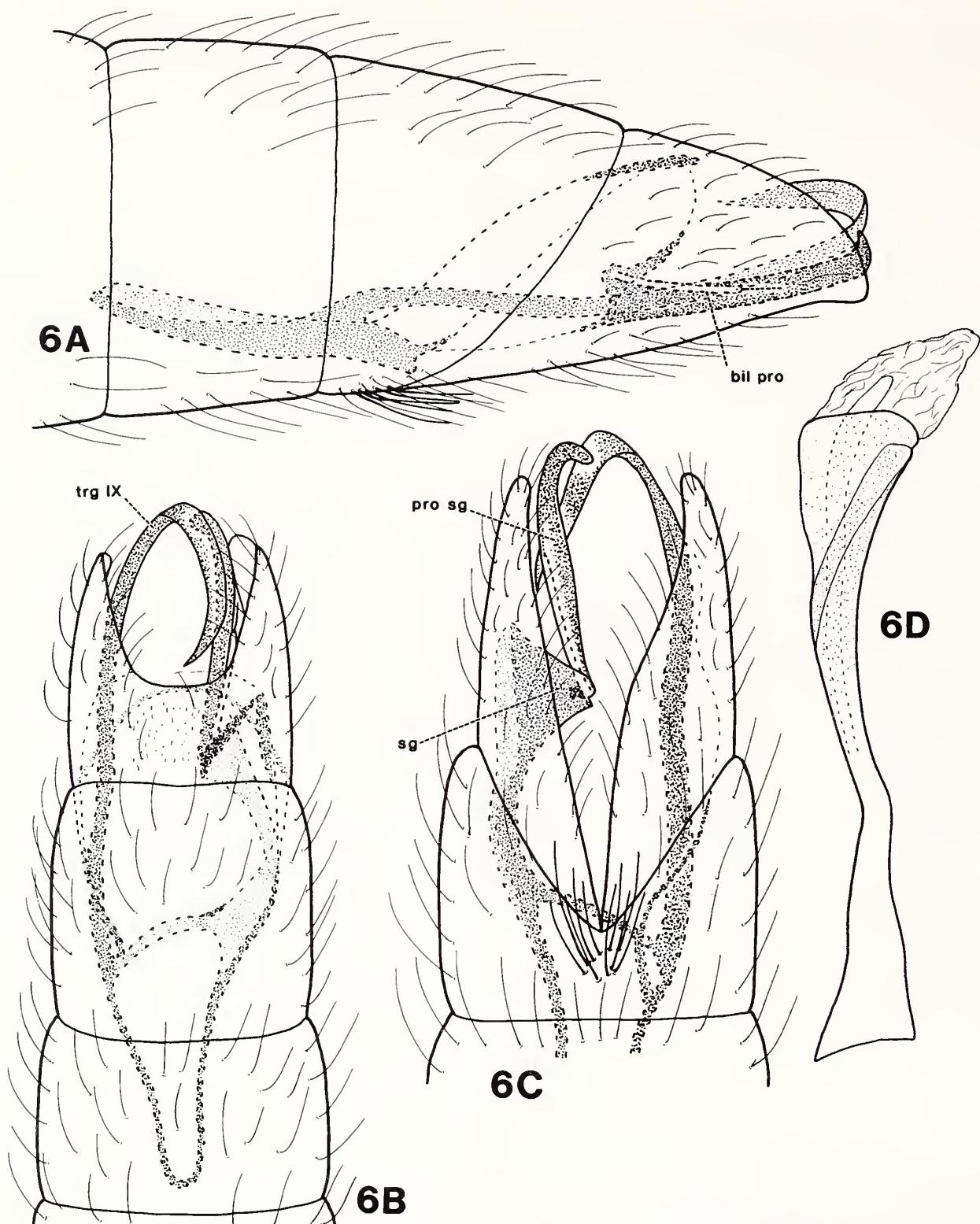


Fig. 6. *Oxyethira rareza*, new species, male genitalia. A. Lateral. B. Dorsal. C. Ventral. D. Phallus, lateral. Abbreviations: bil pro = bilobed process; pro sg = process of subgenital plate; sg = subgenital plate; trg IX = tergum IX.

bearing mesal excavation, right arm rectangular, sinuate along mesal margin. Bilobed processes lacking. Phallus short, stout; with pair of lateral, sclerotized rods—left rod thick, curving dorsally; right rod angled at midlength, subapicoventral margin serrate.

*Holotype*. Male, COSTA RICA: GUANACASTE: Quebrada Garcia, 10.6 km ENE Quebrada Grande, 10.862°N, 85.428°W, el. 470 m, 8.iii.1986, Holzenthal and Fasth (NMNH).

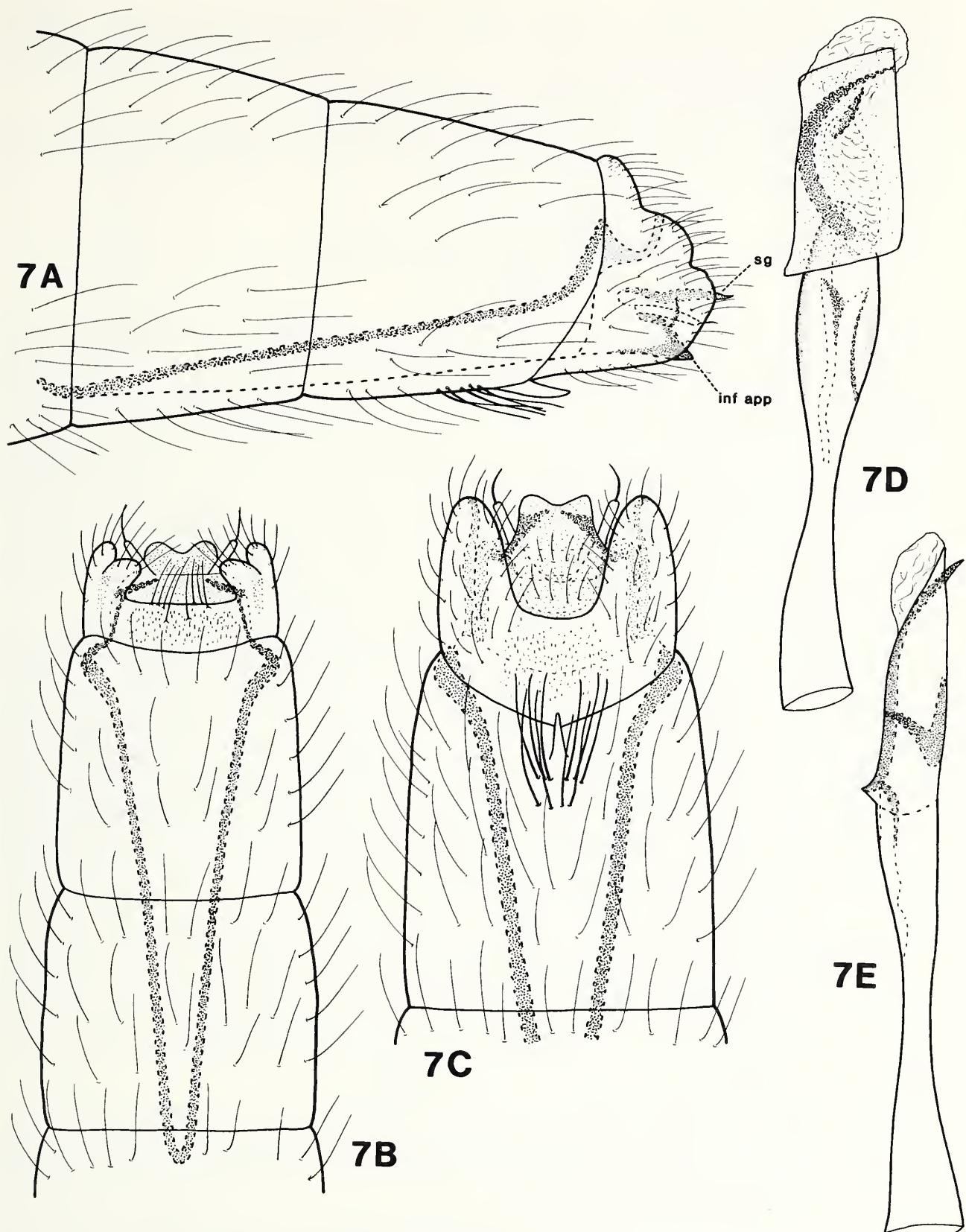


Fig. 7. *Oxyethira sencilla*, new species, male genitalia. A. Lateral. B. Dorsal. C. Ventral. D. Phallus, lateral. E. Phallus, ventral. Abbreviations as in Figures 1 and 2.

**Paratypes.** Same data as holotype, 96 males (UMSP); ALAJUELA: Reserva Forestal San Ramón, Río San Lorencito and trib., 10.216°N, 84.607°W, el. 980 m, 30.iii-1.iv.1987, Holzenthal, Hamilton, Heyn, 7 males (INBIO); CARTAGO: Quebrada Plantanillo, 5 km E Moravia de Chirripó, 9.821°N, 83.407°W, el. 1,130 m, 7.viii.1987,

Holzenthal, Morse, Clausen, 1 male (UMSP); PUNTARENAS: Río Singrí, 2 km S Finca Helechales, 9.057°N, 83.082°W, el. 720 m, 21.ii.1986, Holzenthal, Morse, Fasth, 2 males (UAL); Río Guineal, 1 km S Finca Helechales, 9.076°N, 83.092°W, el. 840 m, Holzenthal, Morse, Fasth, 3 males (UMSP).

**Etymology.** Spanish: “little saw,” referring to the serrate posterior margin of segment VIII of this species.

### Oxyethira tica, new species

Figs. 9, 10

This species, a member of the Azteca Group of the subgenus *Loxotrichia*, is very similar in overall appearance to *O. janella* Denning and *O. puertoricensis* Flint. Males of the new species are distinguished by the acute, elongate process on the ventrolateral margin of segment VIII which is absent in *O. janella* and enlarged in *O. puertoricensis*. In the females, the ventral processes supporting the oviduct (Fig. 10C, D) are short in the new species and elongate in both *O. janella* (Fig. 10E, F) and *O. puertoricensis*.

Previously published records of *O. janella* from Costa Rica (Bueno-Soria and Flint, 1978; Holzenthal, 1988) probably represent misidentifications of *O. tica*. To date, we have not seen *O. janella* from mainland Costa Rica, although it is known from Cocos Island in the Pacific Ocean, about 500 km southwest of the mainland.

**Male.** Length 2.2–3.1 mm. Brown in alcohol. Antennae with 34 segments. Genitalia as in Figure 9. Abdominal sternum VII with short, apicomosal process. Segment VIII produced slightly midlaterally into segment VII, anterior margin with ventrolateral process, extending almost to length of dorsolateral lobe and narrowing to acute apex; VIII deeply excised ventrally with acute lateral lobes flaring slightly outward; dorsally with U-shaped mesal excision. Segment IX elongate posteriorly, bearing setose process, with shallow notch at apex. Inferior appendages indistinct and fused with segment IX. Subgenital plate elongate, narrowing posteriorly to acute apex; bilobed processes closely appressed and about half length of subgenital plate. Phallus tubular with several indistinct folds at apex. **Female.** Length 2.2–2.4 mm. Antennae with 25 segments. Similar in overall appearance to male. Genitalia as in Figure 10. Apodemes of segment VIII short. Segments IX and X short and apparently fused dorsally, bearing pair of cerci at apex. Oviduct supported by paired posteroventrally extended rods which are about twice the length of the spermathecal sclerite; posterior ring sclerite thin, curved in lateral view.

**Holotype.** Male, COSTA RICA: GUANACASTE: Parque Nacional Santa Rosa, Quebrada El Duende, near La Casona, 10.838°N, 85.614°W, el. 280 m, 29.vi.1986, Holzenthal, Heyn, Armitage (NMNH).

**Paratypes.** COSTA RICA: ALAJUELA: Río Pizote, 5 km N Dos Ríos, 10.948°N, 85.291°W, el. 470 m, 9.iii.1986, Holzenthal and Fasth, 2 males (UMSP); Río Pizote, 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth, 17 males (UMSP). GUANACASTE: Parque Nacional Rincón de la Vieja, Quebrada Agua Apinolada, 10.759°N, 85.292°W, el. 795 m, 25.vi.1986, Holzenthal, Heyn, Armitage, 2 males (INBIO); Parque Nacional Guanacaste, Estación Pitilla, Río Orosí, 10.991°N, 85.428°W, el. 700 m, 19–20.vi.1988, C. M. and O. S. Flint, R. Holzenthal, 1 male (INBIO); Parque Nacional Guanacaste, El Hacha, Quebrada Alcornoque, 11.009°N, 85.577°W, el. 250 m, 26.vii.1987, Holzenthal, Morse, Clau-

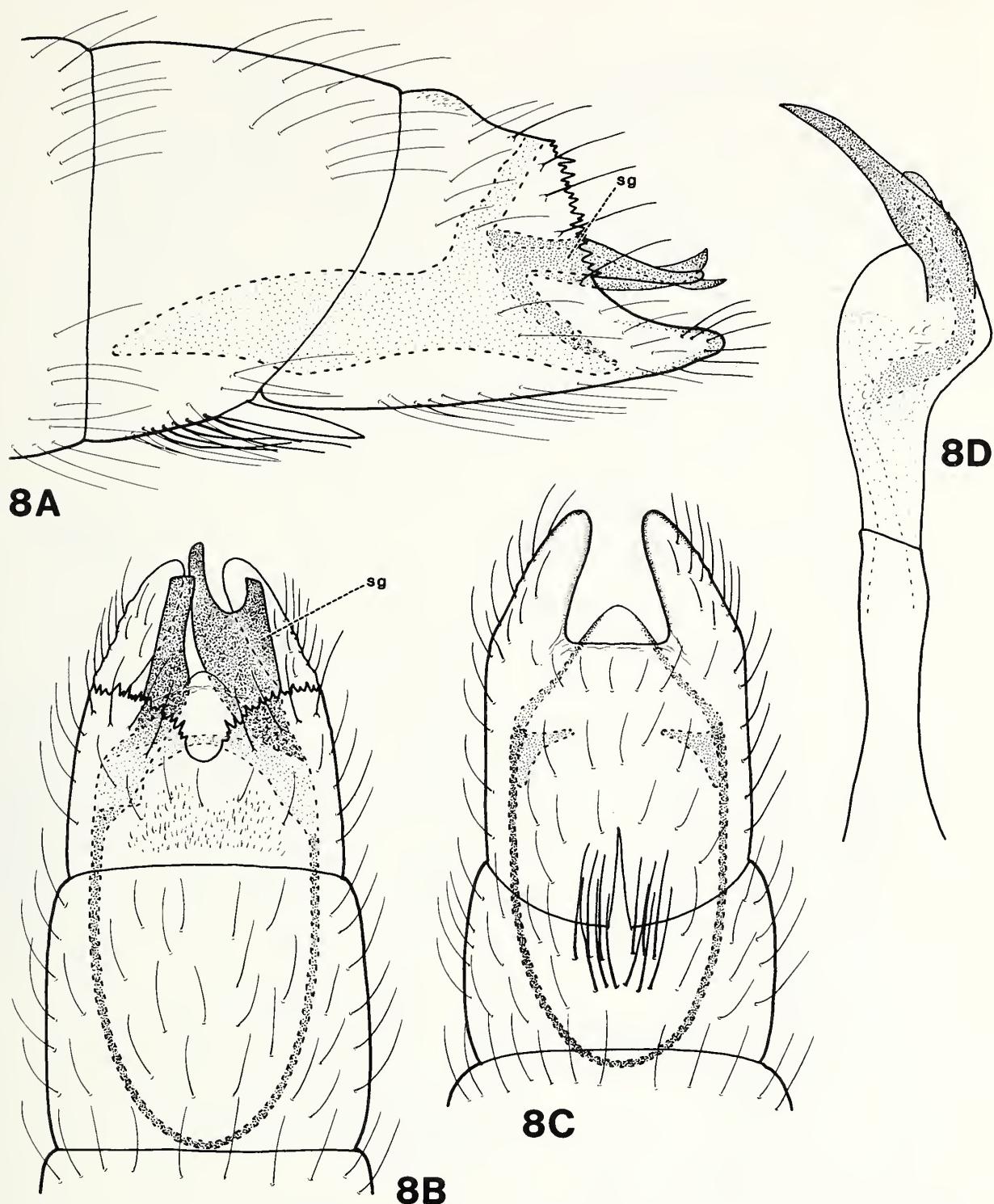


Fig. 8. *Oxyethira sierruca*, new species, male genitalia. A. Lateral. B. Dorsal. C. Ventral. D. Phallus, lateral. Abbreviations as in Figures 1 and 2.

sen, 1 male (UAL); Quebrada Garcia, 10.6 km ENE Quebrada Grande, 10.862°N, 85.428°W, el. 470 m, 8.iii.1986, Holzenthal and Fasth, 1 male (UAL); Río Los Ahogados, 11.3 km ENE Quebrada Grande, 10.865°N, 85.423°W, el. 470 m, 7.iii.1986, Holzenthal and Fasth, 2 males (UMSP); Río Mena, 4.2 km W Santa Cecilia, 11.059°N, 85.448°W, el. 260 m, 11.iii.1986, Holzenthal and Fasth, 1 male (UMSP); Río Tempisquito, 3 km S route 1, 10.790°N, 85.552°W, el. 75 m, 6.iii.1986, Holzenthal and Fasth, 1 male (UMSP); Río Tizate, 7.2 km NE Cañas Dulces, 10.773°N, 85.449°W, el. 275 m, 28.vi.1986, Holzenthal, Heyn, Armitage, 1 male (UMSP). HEREDIA:

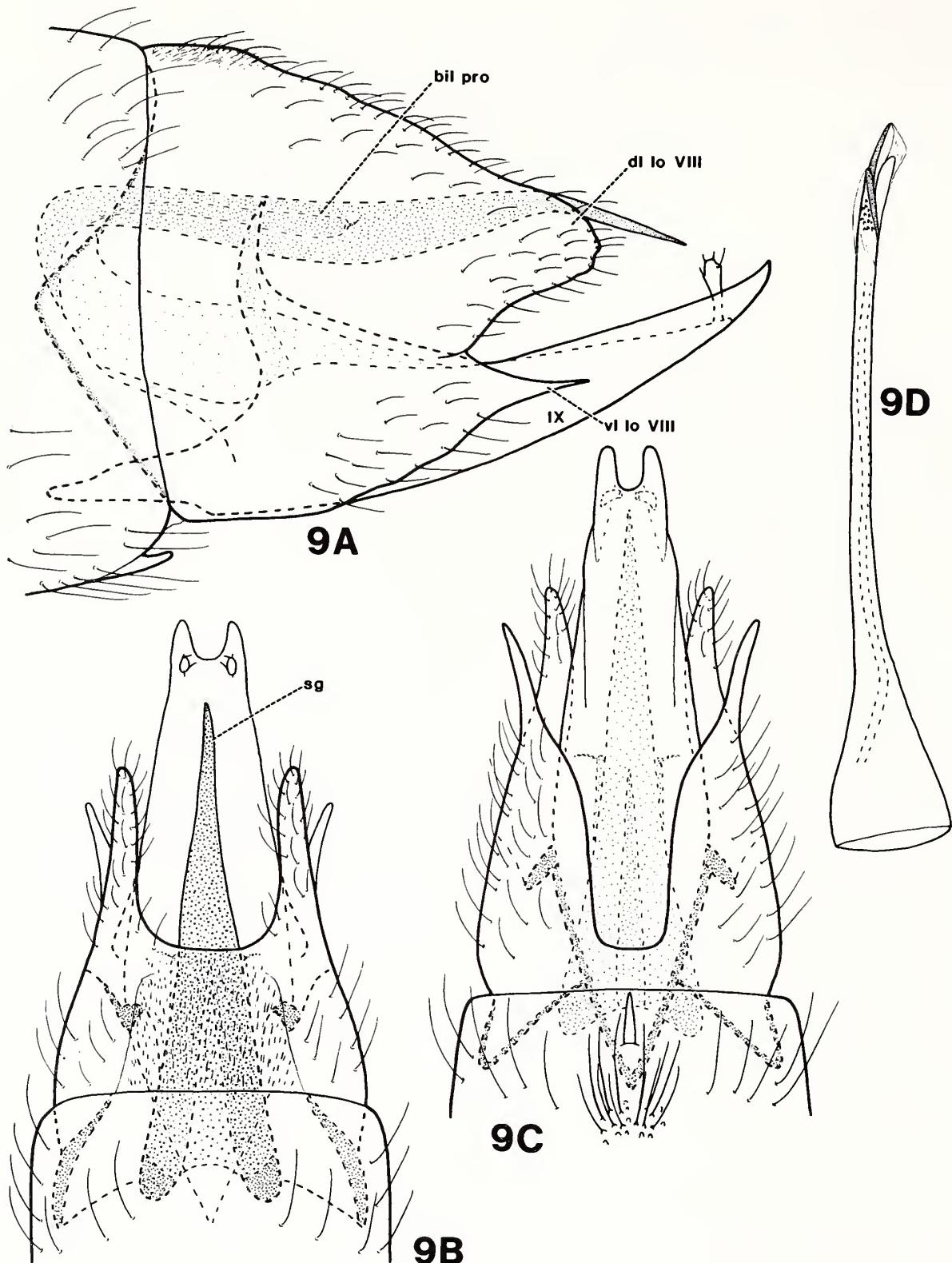


Fig. 9. *Oxyethira tica*, new species, male genitalia. A. Lateral. B. Dorsal. C. Ventral. D. Phallus, lateral. Abbreviations: dl lo VIII = dorsolateral lobe of segment VIII; vl lo VIII = ventrolateral lobe of segment VIII; others as in Figure 2.

Río Bijagual on road to Magsasay, 10.408°N, 84.076°W, el. 140 m, 12.ii.1986, Holzenthal, Morse, Fasth, 1 male (UMSP). LIMON: Río Telire and small trib., SE Suretka, 9.554°N, 82.892°W, el. 48 m, 1.ii.1986, Holzenthal, Morse, Fasth, 1 male (UMSP); Río Uatsi, 8 km (air) W Bribri, 9.62°N, 82.90°W, el. 60 m, 25.iii.1987, Holzenthal, Hamilton, Heyn, 5 males (UMSP). PUNTARENAS: 2.8 mi E of Golfito,

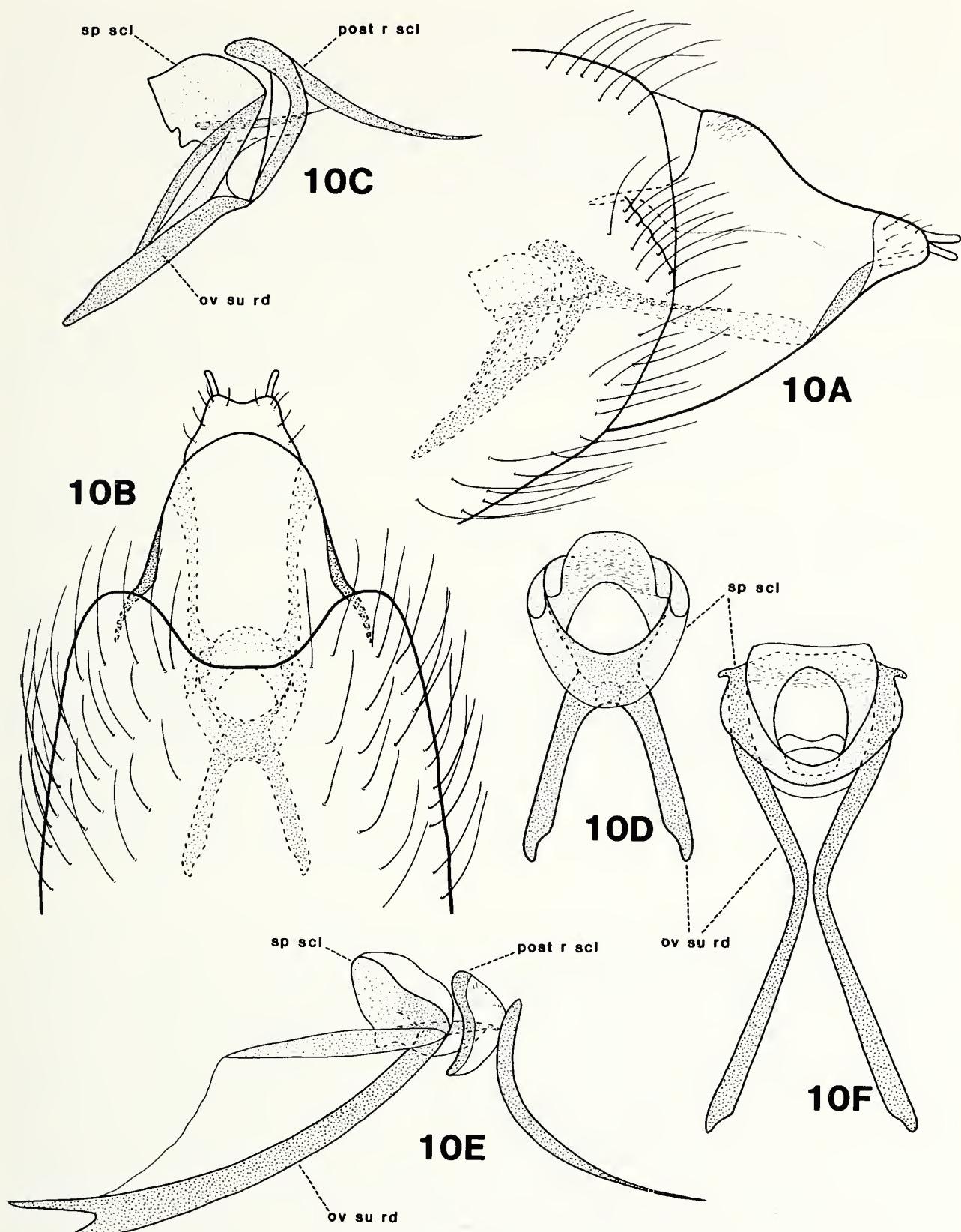


Fig. 10. *Oxyethira* spp., female genitalia. A–D. *Oxyethira tica*, new species. A. Lateral. B. Ventral. C. Internal sclerites, lateral. D. Same, ventral. E–F. *Oxyethira janella* Denning. E. Internal sclerites, lateral. F. Same, ventral. Abbreviations: ov su rd = oviduct support rod; post r scl = posterior ring sclerite; sp scl = spermathecal sclerite.

18–19.vii.1967, O. S. Flint, Jr., 1 male (NMNH); Quebrada Pita, 3 km (air) W Golfito, 8.642°N, 83.193°W, el. 15 m, 15.ii.1986, Holzenthal, Morse, Fasth, 1 male (UMSP); Río Ceibo, route 2, 6 km W rd. to Buenos Aires, 9.149°N, 83.377°W, el. 250 m, 20.ii.1986, Holzenthal, Morse, Fasth, 1 male (INBIO); Río Singrí, 2 km (air) S Finca Helechales, 9.057°N, 83.082°W, el. 720 m, 21.ii.1986, Holzenthal and Fasth, 2 males (UMSP). SAN JOSÉ: Parque Nacional Braulio Carrillo, Estación Carrillo, Quebrada Sanguijuela, 10.160°N, 83.963°W, el. 800 m, 27.iii.1987, Holzenthal, Hamilton, Heyn, 1 male (UMSP); Río General, 1 mi S San Isidro, 1.vii.1967, P. J. Spangler, 1 male (NMNH); Río Negro, 3.5 km SE jct. route 239, 9.680°N, 84.394°W, el. 230 m, 21.iii.1986, Holzenthal and Fasth, 1 male (UMSP).

*Etymology.* Named for the Costa Ricans, or “Ticos,” in recognition of the warm hospitality they have extended to the senior author and his associates during their research in the country.

#### DISTRIBUTION RECORDS FOR *OXYETHIRA* IN COSTA RICA

*Oxyethira arizona* Ross, 1948:202, fig. 4, male, United States: Arizona (INHS); Bueno-Soria and Flint, 1978:204; Bickle, 1979:54, fig. 158; Kelley, 1984:439; Holzenthal, 1988:62 (*arizonica*, *lapsus*).

*Records.* ALAJUELA: Reserva Forestal San Ramón, Río San Lorencito and trib., 10.216°N, 84.607°W, el. 980 m, 13–16.vi.1988, C. M. and O. S. Flint, R. Holzenthal, 1 male. GUANACASTE: Río Tempisque, 3 km S route 1, 10.790°N, 85.552°W, el. 75 m, 6.iii.1986, Holzenthal and Fasth, 2 males; Parque Nacional Guanacaste, Maritza, Río Tempisque, 10.958°N, 85.497°W, el. 550 m, 19–20.vii.1987, Holzenthal, Morse, Clausen, 1 male.

*Oxyethira azteca* (Mosely) 1937:165, fig. 13, male, Mexico (*Loxotrichia*) (BMNH); Flint, 1968:54, fig. 138–139, 149; Bueno-Soria and Flint, 1978:205; Holzenthal, 1988:62.

*Records.* ALAJUELA: Río Pizote, 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth, 184 males; Río Pizote, 5 km N Dos Rios, 10.948°N, 85.291°W, el. 470 m, 9.iii.1986, Holzenthal and Fasth, 446 males. CARTAGO: Río Platanillo, 2.2 km E Tayutic, 9.82°N, 83.55°W, el. 730 m, 30.i.1986, Holzenthal, Morse, Fasth, 1 male. GUANACASTE: Río Mena, 4.2 km W Santa Cecilia, 11.059°N, 85.448°W, el. 260 m, 11.iii.1986, Holzenthal and Fasth, 46 males. HEREDIA: Est. Biol. La Selva, Quebrada Sura, 10.437°N, 84.010°W, el. 50 m, 20–21.vi.1986, Holzenthal, Heyn, Armitage, 7 males; Est. Biol. La Selva, Río Puerto Viejo, 10.440°N, 84.012°W, el. 30 m, 19.vi.1986, Holzenthal, Heyn, Armitage, 4 males; Río Bijagual, road to Magsasay, 10.408°N, 84.076°W, el. 140 m, 12.ii.1986, Holzenthal, Morse, Fasth, 536 males; Río Sarapiquí, 7 km W Puerto Viejo, 10.452°N, 84.067°W, el. 50 m, 11.ii.1986, Morse and Fasth, 18 males. PUNTARENAS: Río Ceibo, route 2, 6 km W rd. to Buenos Aires, 9.149°N, 83.377°W, el. 250 m, 20.ii.1986, Holzenthal, Morse, Fasth, 76 males; Río Singrí, 2 km (air) S Finca Helechales, 9.057°N, 83.082°W, el. 720 m, 21.ii.1986, Holzenthal, Morse, Fasth, 3 males; SAN JOSE: Río General, 1 mi S San Isidro, 1.vii.1967, P. J. Spangler, 5 males (NMNH).

*Oxyethira costaricensis* Kelley, 1983:44, fig. 4, male, Costa Rica (NMNH); Holzenthal, 1988:62.

*Record.* HEREDIA: Los Cartagos, 24.vi.1967, P. J. Spangler, male holotype (NMNH). Note: This species is known only from the male holotype.

*Oxyethira glasa* (Ross) 1941:70, fig. 28, male, United States: Oklahoma (*Loxotrichia*) (INHS); Blickle, 1979:54, fig. 160; Holzenthal, 1988:63.

*Records.* ALAJUELA: Río Pizote, 5 km N Dos Ríos, 10.948°N, 85.291°W, el. 470 m, 9.iii.1986, Holzenthal and Fasth, 2 males.

*Oxyethira janella* Denning, 1948:397, fig. 2A–B, male, United States: Florida (D. G. Denning collection); Flint, 1968a:52, figs. 136–137, 148; Bueno-Soria and Flint, 1978:205 (record suspect); Holzenthal, 1988:63 (record suspect).

*Record.* COSTA RICA: Isla del Coco: 500 km SW [mainland] Costa Rica, Chatham Bay, at light, 8–10.iv.1979, R. Silberglied, 1 male (LACM).

*Oxyethira parazteca* Kelley, 1983:53, fig. 16, male, Ecuador (NMNH); Kelley, 1984: 442; Holzenthal, 1988:63.

*Records.* ALAJUELA: Río Pizote, 5 km N Dos Ríos, 10.948°N, 85.291°W, el. 470 m, 9.iii.1986, Holzenthal and Fasth, 20 males; Río Pizote, 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth, 3 males. CARTAGO: Quebrada Platanillo, 5 km E Moravia de Chirripó, 9.821°N, 83.407°W, el. 1,130 m, 7.viii.1987, Holzenthal, Morse, Clausen, 2 males; Río Platanillo, 2.2 km E Tayutic, 9.82°N, 83.55°W, el. 730 m, 30.i.1986, Holzenthal, Morse, Fasth, 2 males. GUANACASTE: P.N. Rincón de la Vieja, Quebrada Agua Apinolada, 10.759°N, 85.292°W, el. 795 m, 25.vi.1986, Holzenthal, Heyn, Armitage, 38 males; Río Góngora (sulfur mine), 4 km (air) NE Quebrada Grande, 10.887°N, 85.470°W, el. 590 m, 21.vii.1987, Holzenthal, Morse, Clausen, 4 males.

*Oxyethira parce* (Edwards and Arnold) 1961:405, figs. 23–25, United States: Texas (*Protoptila*) (S. W. Edwards collection).

*Records.* ALAJUELA: P.N. Rincón de la Vieja, Quebrada Provisión, 10.769°N, 85.281°W, el. 810 m, 4.iii.1986, Holzenthal and Fasth, 3 males; Reserva Forestal San Ramón, Río San Lorencito and trib., 10.216°N, 84.607°W, el. 980 m, 30.iii–1.iv.1987, Holzenthal, Hamilton, Heyn, 2 males; same, except 13–16.vi.1988, C. M. and O. S. Flint, Holzenthal, 1 male; Río Pizote, 5 km (air) S Brasilia, 10.972°N, 85.345°W, el. 390 m, 12.iii.1986, Holzenthal and Fasth, 2 males. CARTAGO: Chitaría, 19.vi.1967, Flint and Ortiz, 4 males, 10 females (NMNH); Quebrada Platanillo, 5 km E Moravia de Chirripó, 9.821°N, 83.407°W, el. 1,130 m, 7.viii.1987, Holzenthal, Morse, Clausen, 5 males; Reserva Tapantí, Río Grande de Orosí, 9.686°N, 83.756°W, el. 1,650 m, 18–21.iii.1987, Holzenthal, Hamilton, Heyn, 1 male; Turrialba, 26.viii.1972, G. F. and S. Hevel, 1 male, 1 female (NMNH). GUANACASTE: Parque Nacional Guanacaste, Estación Pitilla, Río Orosí, 10.99°N, 85.428°W, el. 700 m, 19–20.vi.1988, C. M. and O. S. Flint, Holzenthal, 16 males, 8 females; P.N. Rincón de la Vieja, Quebrada Agua Apinolada, 10.759°N, 85.292°W, el. 795 m, 25.vi.1986, Holzenthal, Heyn, Armitage, 2 males; P.N. Santa Rosa, Quebrada El Duende, nr La Casona, 10.838°N, 85.614°W, el. 280 m, 29.vi.1986, Holzenthal, Heyn, Armitage, 1 male; Quebrada Garcia, 10.6 km ENE Quebrada Grande, 10.862°N, 85.428°W, el. 470 m, 8.iii.1986, Holzenthal and Fasth, 2 males; Río Góngora (sulfur

mine), 4 km (air) NE Quebrada Grande, 10.887°N, 85.470°W, 21.vii.1987, Holzenthal, Morse, Clausen, 2 males; Río Tizate, 7.2 km NE Cañas Dulces, 10.773°N, 85.449°W, el. 275 m, 28.vi.1986, Holzenthal, Heyn, Armitage, 11 males. HEREDIA: Río Bijagual, road to Magsasay, 10.408°N, 84.076°W, el. 140 m, 12.ii.1986, Holzenthal, Morse, Fasth, 17 males. LIMON: La Lola near Matina, 11.iii.1965, S. and W. D. Duckworth, 1 male (NMNH); Reserva Biol. Hitoy-Cerere, Río Cerere, 9.671°N, 83.028°W, el. 90 m, 23–24.iii.1987, Holzenthal, Hamilton, Heyn, 27 males; Río Banano, 16 km WSW Bomba, 9.888°N, 83.167°W, el. 150 m, 26.iii.1987, Holzenthal, Hamilton, Heyn, 3 males; Río Telire and small trib., SE Suretka, 9.554°N, 82.892°W, el. 48 m, 1.ii.1986, Holzenthal, Morse, Fasth, 11 males. PUNTARENAS: 2.8 mi E Golfito, 18–19.vii.1967, O.S. Flint, Jr., 3 males, 7 females (NMNH); Quebrada Pita, 3 km (air) W Golfito, 8.642°N, 83.193°W, el. 15 m, 15.ii.1986, Holzenthal, Morse, Fasth, 28 males; Río Bellavista, 1.5 km NW Las Alturas, 8.951°N, 82.846°W, el. 1,400 m, 8–9.iv.1987, Holzenthal, Hamilton, Heyn, 31 males; Río Ceibo, route 2, 6 km W rd. to Buenos Aires, 9.149°N, 83.377°W, el. 250 m, 20.ii.1986, Holzenthal, Morse, Fasth, 27 males; Río Cotón in Las Alturas, 8.938°N, 82.826°W, el. 1,360 m, 16.ii.1986, Holzenthal, Morse, Fasth, 1 male; Río Guineal, 1 km (air) E Finca Helechales, 9.076°N, 83.092°W, el. 840 m, 22.ii.1986, Holzenthal, Morse, Fasth, 14 males; Río Jaba at rock quarry, 1.4 km (air) W Las Cruces, 8.79°N, 82.97°W, el. 1,150 m, 14.vi.1986, Holzenthal, Heyn, Armitage, 23 males; Río Jaba, 2.4 km (air) NW San Vito, 8.832°N, 82.991°W, el. 970 m, 13.vi.1986, Holzenthal, Heyn, Armitage, 5 males; Río Singrí, 2 km (air) S Finca Helechales, 9.057°N, 83.082°W, el. 720 m, 21.ii.1986, Holzenthal, Morse, Fasth, 73 males. SAN JOSE: Pacuare, Río General, 1.vii. 1967, Flint and Ortiz, 2 males, 5 females (NMNH); Río General, 1 mi S San Isidro, 1.vii.1967, P. J. Spangler, 9 males, 27 females (NMNH); Río Negro, 3.5 km SE jct. route 239, 9.68°N, 84.394°W, el. 230 m, 21.iii.1986, Holzenthal and Fasth, 1 male.

*Oxyethira simulatrix* Flint, 1968:43, figs. 89–91, 99, male, Jamaica (NMNH); Holzenthal, 1988:63.

**Records.** GUANACASTE: Parque Nacional Guanacaste, Maritza, Río Tempisque, 10.958°N, 85.497°W, el. 550 m, 19–20.vii.1987, Holzenthal, Morse, Clausen, 1 male; Río Tempisque, 3 km S route 1, 10.790°N, 85.522°W, el. 75 m, 6.iii.1986, Holzenthal and Fasth, 1 male. LIMON: Río Telire and small trib., SE Suretka, 9.554°N, 82.892°W, el. 48 m, 1.ii.1986, Holzenthal, Morse, Fasth, 11 males. PUNTARENAS: Río Ceibo, route 2, 6 km W rd. to Buenos Aires, 9.149°N, 83.377°W, el. 250 m, 20.ii.1986, Holzenthal, Morse, Fasth, 1 male; Río Singrí, 2 km (air) S Finca Helechales, 9.057°N, 83.082°W, el. 720 m, 21.ii.1986, Holzenthal, Morse, Fasth, 1 male. SAN JOSE: P.N. Braulio Carrillo, Quebrada Sanguijuela, Est. Carrillo, 10.160°N, 83.963°W, el. 800 m, 27.iii.1987, Holzenthal, Hamilton, Heyn, 1 male; Río General, 1 mi S San Isidro, 1.vii.1967, P. J. Spangler, 1 male (NMNH).

#### KEY TO MALES OF COSTA RICAN *OXYETHIRA*

1. Inferior appendages absent or vestigial (Figs. 6A, C); subgenital plate asymmetrical (Figs. 6C, 8B) ..... 2
- Inferior appendages present (Figs. 5A, C, 3A, C); subgenital plate symmetrical (Fig. 2C) or absent ..... 3
- 2(1). Antennae with less than 40 segments; subgenital plate asymmetrical and well

- developed only on left side (Fig. 6C); tergum IX a long, narrow, ribbonlike band (Fig. 6B); segment VIII smooth dorsally (Fig. 6B) ..... *O. rareza*, n. sp.
- Antennae with more than 40 segments; subgenital plate asymmetrical and well developed on both sides (Fig. 8B); tergum IX reduced to thin band (Figs. 8A, B); segment VIII serrate dorsally (Fig. 8B) ..... *O. sierruca*, n. sp.
- 3(1). Inferior appendages elongate, thin and fingerlike (Kelley, 1983, figs. 4a, b) .....  
..... *O. costaricensis* Kelley
- Inferior appendages variable, but not thin and fingerlike (Figs. 3A, 5A, 7A, 9A) 4
- 4(3). Segment IX short, extending anteroventrally into segment VII (Figs. 1A, 9A), often broadly rounded posteriorly in ventral view (Fig. 1C) ..... 5
- Segment IX elongate, extending anteroventrally into segment VI (Fig. 5A) or V (Fig. 7A), usually narrowing posteriorly in ventral view (Fig. 4C) ..... 13
- 5(4). Subgenital plate short in lateral view (Ross, 1948, figs. 4, 4a; Flint, 1968a, fig. 89), wide in ventral view (Fig. 1C); inferior appendages short in lateral view (Fig. 1A; Ross, 1948, figs. 4, 4a) ..... 6
- Subgenital plate elongate in lateral view (Fig. 9A; Flint, 1991, figs. 134, 135, 138), triangular in dorsal view (Fig. 9B); inferior appendages elongate in lateral and ventral views (Figs. 9A, C) ..... 9
- 6(5). Segment VIII with deep, V-shaped mesal incision ventrally (Fig. 2C); inferior appendages in ventral view elongate, rectangular and separate (Fig. 2C) .....  
..... *O. apinolada*, n. sp.
- Segment VIII with shallow, rounded mesal incision ventrally; inferior appendages in ventral view fused, short (Flint, 1968a, fig. 91; Ross, 1948, fig. 4a) ..... 7
- 7(6). Dorsolateral process of segment VIII slender, narrowing posteriorly (Ross, 1948, fig. 4) ..... 8
- Dorsolateral process of segment VIII broad basally, upcurved and bearing stout spine at apex (Ross, 1941, fig. 28) ..... *O. glasa* (Ross)
- 8(7). Phallus tubular with ejaculatory duct protruding and distally recurved (Flint, 1968a, fig. 90) ..... *O. simulatrix* Flint
- Phallus divided into central tubular lobe bearing ejaculatory duct and lateral lobe encircling the shaft (Ross, 1948, figs. 4b, c) ..... *O. arizona* Ross
- 9(5). Segment VIII with prominent dorsolateral lobe, incised medially (Figs. 9A, B; Mosely, 1937, fig. 3b); subgenital plate elongate and triangular in dorsal view, in lateral view curving ventrad distally (Figs. 9A, B) ..... 10
- Segment VIII without dorsolateral lobe, no incision medially; subgenital plate short and less triangular in dorsal view, in lateral view curving dorsad distally (Kelley, 1983, fig. 16) ..... *O. parazteca* Kelly
- 10(9). Inferior appendages in ventral view with wide, V-shaped excision at apex (Mosely, 1937, fig. 13); bilobed processes of subgenital plate prominent ..... 11
- Inferior appendages in ventral view with shallow, rounded excision at apex (Fig. 9C); bilobed processes of subgenital plate indistinct (Fig. 9B) ..... 12
- 11(10). Dorsal process of segment IX originating at midlength; bilobed process about half length of subgenital plate; phallus with apicoventral lip short (Flint, 1991, figs. 138–140) ..... *O. azteca* (Mosely)
- Dorsal process of segment IX originating anteriorly of midlength; bilobed process greater than half length of subgenital plate; phallus with apicoventral lip elongate (Flint, 1991, figs. 134–137) ..... *O. parce* (Edwards and Arnold)
- 12(10). Segment VIII with ventrolateral lobe small and rounded posteriorly (Flint, 1968a, fig. 81) ..... *O. janella* Denning<sup>2</sup>

<sup>2</sup> Not seen from mainland Costa Rica during this study. Literature records of *O. janella* from the mainland need to be reexamined in light of the discovery of *O. tica*.

- Segment VIII with ventrolateral lobe elongate and narrowing to an acute tip posteriorly (Fig. 9A) ..... *O. tica*, n. sp.
- 13(4). Segment VIII with dorsolateral processes (Figs. 2A, 4A, 5A) ..... 14
- Segment VIII without dorsolateral processes (Figs. 3A, 7A) ..... 16
- 14(13). Processes of segment VIII arising dorsobasally (Figs. 4A, 5A) ..... 15
- Processes of segment VIII dorsolateral in position, not basal or anterior (Fig. 2A) ..... *O. cuernuda*, n. sp.
- 15(14). Dorsobasal processes of segment VIII bearing numerous thick spines, widely separated basally, then converging distally (Fig. 4B); phallus bearing two simple, sclerotized lateral processes (Fig. 4D) ..... *O. espinada*, n. sp.
- Dorsobasal processes of segment VIII lacking spines, narrowly separated basally and only slightly convergent distally (Fig. 5B); phallus with sclerotized lateral processes divided at apex, with dorsal arm thin and elongate (Figs. 5D, E) ..... *O. hilosa*, n. sp.
- 16(13). Segment IX extending anteriorly to middle of segment VI, bearing narrow, elongate dorsolateral processes (Fig. 3A); inferior appendages elongate (Fig. 3C); subgenital plate absent; phallus tubular, lacking sclerotized processes (Fig. 3D) ..... *O. culebra*, n. sp.
- Segment IX extending anteriorly into segment V, lacking dorsolateral processes (Fig. 7A); inferior appendages short (Figs. 7A, C); subgenital plate prominent (Fig. 7A); phallus with pair of sclerotized distal processes (Figs. 7D, E) *O. sencilla*, n. sp.

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## ON THE SPIDER SUBFAMILY ZAVATTARICINAE (ARANAEAE, GNAPHOSIDAE)

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*Abstract.*—The spider genus *Zavattarica* Caporiacco, and the monogenic subfamily Zavattaricinæ, were based on the supposed presence of a reduced number of spinnerets. However, both described species actually have the normal gnaphosid complement of six spinnerets, and *Zavattarica* Caporiacco is placed as a junior synonym of *Zelotes* Gistel.

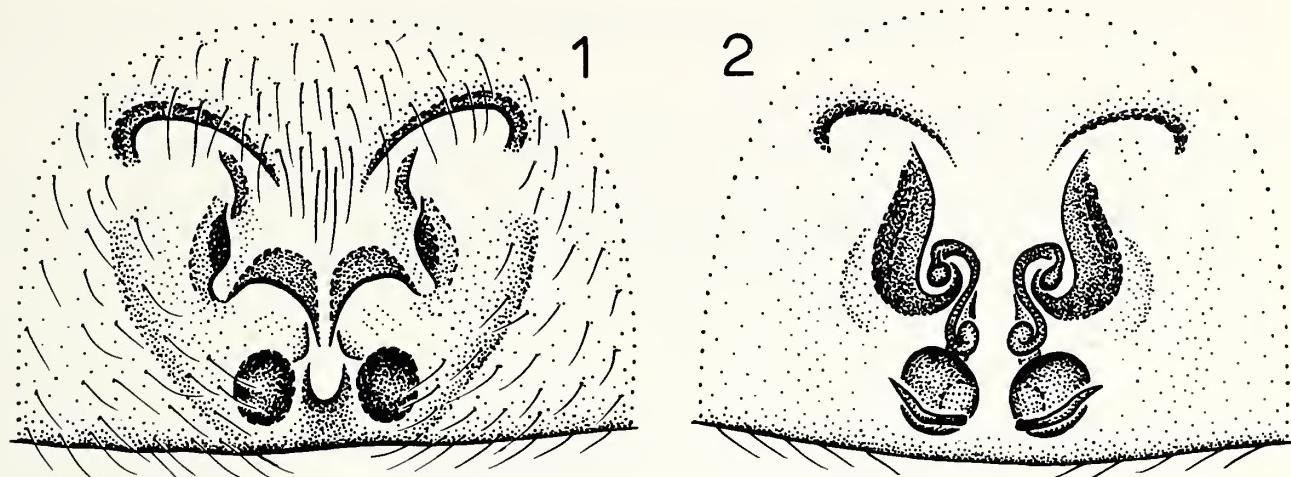
Caporiacco (1941) established a new subfamily of gnaphosid spiders, the Zavattaricinæ, for a new genus and species, *Zavattarica bimamillata*, based on a single female from Ethiopia. The new genus and subfamily were said to differ from all other gnaphosids in having only two spinnerets (the “inferiori” or anterior lateral pair). Subsequently, Caporiacco (1947) expanded the diagnosis of the group, describing a second species, *Zavattarica tetramamillata*, based on two females from Tanzania, supposedly differing from the type species and all other gnaphosids in having only four spinnerets (including the “superiores” or posterior lateral pair).

The existence of this subfamily was recognized in the catalog of Roewer (1955), and maintained in the supplement to that catalog by Brignoli (1983). Aside from those catalog citations, however, there seems to have been no significant mention of these taxa in the subsequent literature.

Through the courtesy of Ms. Sarah Mascherini of the Museo Zoologico de “La Specola” in Firenze, Italy, I have recently had the opportunity to examine the holotype of *Z. bimamillata*. During a recent visit to the laboratory of Dr. Vladimir I. Ovtsharenko at the Zoological Institute, USSR Academy of Sciences, Leningrad, I also had the opportunity to examine type material of *Z. tetramamillata*, which had been borrowed by Dr. Ovtsharenko from the Hungarian National Museum in Budapest.

In both cases, Caporiacco’s observations on the spinnerets are simply erroneous. Six spinnerets are present in these specimens. The posterior median and posterior lateral pairs are inconspicuous, because they are partially contracted into the abdomen, but they are clearly present. The spiders have the metatarsal preening combs typical of zelotine gnaphosids (Platnick and Shadab, 1982:figs. 1, 2), and epigyna typical of the genus *Zelotes* Gistel (see figs. 1, 2, prepared with the help of Dr. Mohammad U. Shadab of the American Museum of Natural History). *Zavattarica* is therefore here placed as a junior synonym of *Zelotes*, resulting in the new combinations *Zelotes bimamillatus* (Caporiacco) and *Zelotes tetramamillatus* (Caporiacco).

Although no generally accepted subfamilial classification of gnaphosids exists (Platnick, 1990), the worldwide and extremely speciose complex of genera sharing the metatarsal preening comb (including at least *Zelotes*, *Drassyllus* Chamberlin, *Camillina* Berland, *Trachyzelotes* Lohmander, *Urozelotes* Mello-Leitão, and *Setaphis*



Figs. 1, 2. *Zelotes bimamillatus* (Caporiacco), epigynum. 1. Ventral view. 2. Dorsal view.

Simon) has long been informally recognized as a group. Ironically, Caporiacco's completely baseless subfamilial name Zavattaricinæ may live on, for there seems to have been no earlier family-group name based on any of these genera!

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## NOTES AND COMMENTS

*J. New York Entomol. Soc.* 100(1):180–181, 1992

### THE IDENTITY AND SYNONYMY OF *HYDROESSA FUSCA* GERMAR (VELIIDAE: HETEROPTERA)

*Hydroessa fusca* Germar (1838) has been an enigma in modern times, not recognized by any worker since Mayr (1868) who transferred it to the genus *Velia* Latreille without comment. In the Drake Collection (USNM) I found one female, with a Mayr determination label in his handwriting, collected during the Novara Expedition at the Cape of Good Hope, South Africa. This specimen belongs to the species currently known as *Ocellovelia germari* Distant, which must therefore fall as a junior synonym. In the discussion below I substantiate the synonymy.

#### *Ocellovelia fusca* Germar, New Combination

*Hydroessa fusca* Germar, 1838:123 (Location of types unknown.)

*Velia fusca* Mayr, 1868:180.

*Ocellovelia germari* Distant, 1904:436 NEW SYNONYMY. (Type in BMNH.)

*Discussion.* The location or existence of Germar's types is unknown. Horn and Kahle (1935, p. 89) state that the Hemiptera part of his collection is in "Zool. Univ. Mus., Lemberg." Presumably Mayr saw Germar's types or at least knew the species, but unfortunately he gives no discussion. *Ocellovelia* and *Angilia* are the only two South African genera with general facies resembling *Velia* as construed at that time.

The description of *Hydroessa* (now *Microvelia* Westwood) *fusca* by Germar (1838) is very brief, however it contains several characters that provide clues as to its identity even without the determination of Mayr (1868): 1. Each elytra with a basal oblique white streak (the only ones visible in old or greasy specimens of *Ocellovelia germari* Distant), 2. The first two antennal segments basally light, distal two hairy, with dark hairs, 3. Head exserted, 4. Hemelytra a little shorter than abdomen, 4. Venter black, margins fuscous, 5. Legs pallid, knees darker, and 6. Twice the size of *Hydroessa reticulata* Burmeister.

The description matches specimens of *Ocellovelia germari* in the Polhemus Collection, with the exception of the rather rough size indication; however, all other veliid known to occur in the Cape region were also compared to test the possibility that Mayr made a mistake in his determination.

Character 6 immediately eliminates all African *Microvelia* species as they are all smaller or about the same size as *reticulata*, i.e., males 1.5 mm, females 1.6 mm. This character also eliminates *Rhagovelia* and *Angilia* species, all 4.8 mm or larger. All three of these genera match the description poorly in other respects as well. Other veliid species occurring in the Cape region belong to the genera *Ocellovelia* China & Usinger (3.7–4.2 mm), *Pseudovelia* Hoberlandt (2.5 mm), and *Xiphoveloides* Hoberlandt (2.5 mm). As can be seen, the size of *fusca* given by Germar does not match

any of the latter three genera very closely so we must examine other characters for the latter two genera.

*Pseudovelia* species agree in the following: Venter black with fuscous margins; first antennal segment basally pallid. They disagree in the following: Hemelytra with four (2 + 2) oblique diffuse sordid white streaks; head not exserted; distal antennal segments with light colored hairs; hemelytra longer than abdomen.

*Xiphoveloidea* species agree in the following: Hemelytra with oblique basal white streaks. They disagree in the following: Venter black, without fuscous margins; first antennal segment uniformly dark; head not exserted; distal antennal segments with light colored hairs; hemelytra longer than abdomen (macropterous form rare).

The possibility remains that *fusca* could be synonymous with *Ocellovelia distanti* China and Usinger, but this species is rare, and is darker, which does not match Germar's description stating that *fusca* is dorsally fuscous.

The conclusion is that no other veliid matches the description of *fusca* as well as *Ocellovelia germari* Distant, and this species is common in the Cape region; thus, Mayr's determination is supported, and *germari* must fall as a synonym.

Because no type-material of *Hydroessa fusca* Germar is known to exist, and in order to insure stability, I here designate a neotype, to be placed in the U.S. National Museum of Natural History, Washington, D.C. The neotype data is as follows: macropterous male, South Africa, Cape Province, Blinkwater Falls, Table Mt., Cape-town, XI-21-1949, B. Malkin.—John T. Polhemus, University of Colorado Museum, 3115 South York St., Englewood, Colorado, USA 80110.

#### ACKNOWLEDGMENTS

I am indebted to R. C. Froeschner, Smithsonian Institution, U.S. National Museum of Natural History (USNM), Washington, D.C. for the opportunity to study material in the Drake Collection under his care.

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**DISPERSAL OF THE ERGOT FUNGUS  
*CLAVICEPS PURPUREA* BY THE  
LAUXANIID FLY *MINETTIA LUPULINA***

---

Insect visitors of diseased plants may be important in the dispersal of many plant pathogens, and their behavior may be important in the distribution of pathogens in plant populations (A'Brook, 1973; Burdon, 1987; DeNoog, 1988; Roche, pers. comm.). Just as not all insect visitors of flowers are effective pollinators (Schemske and Horvitz, 1984) it is possible that not all visitors of diseased plants are effective dispersers of pathogens. In this study I assess the ability of two insect visitors of the pathogen *Claviceps purpurea* (Fr.) Tul. (Clavicipitaceae) to disperse it to the host plant *Festuca arundinacea* Schreb. (Poaceae).

Although the ascomycetous fungus *Claviceps purpurea* is a well studied, polycyclic pathogen of many species of grasses (Loveless, 1971), the secondary dispersal vectors of this pathogen have not been previously well described. At the time of primary infection, the wind disperses ascospores after sclerotia germinate (Luttrell, 1980). Once ascospores successfully infect the ovaries of grasses, the fungus induces the grasses to produce a sweet liquid called honeydew in which conidia are formed. It has been noted that the honeydew is attractive to insects, and that the fungus is secondarily dispersed by flies and beetles (Mower and Hancock, 1975). I know of no study, however, that quantifies the dispersal abilities of the insect visitors of grasses infected by *C. purpurea*.

At the Mountain Lake Biological Station in western Virginia, I found that individuals of *F. arundinacea* that are infected by *C. purpurea* and producing honeydew are predominantly visited by two insects, a mycophagous fly, *Minettia lupulina* (F.) (Diptera: Lauxaniidae) and a mycophagous beetle, *Acylomus* sp. (Coleoptera: Phalacridae). Because healthy panicles of the grass do not produce nectar or other rewards, it is unknown what causes insects to disperse the pathogen to uninfected individuals.

The beetle visits the infected florets when honeydew is present and sclerotia are just beginning to form. The beetles lay eggs at that time (Lemon, unpubl. data). Beetle larvae develop within the sclerotia. During the early stages of sclerotia development, I found developing beetle larvae, obvious feeding damage, and frass. At the end of the growing season, I found pupae and adult beetles within mature sclerotia as well.

The purpose of this study was to determine if the beetles or flies could be responsible for secondary dispersal of the pathogen. I investigated whether or not these two species carried spores on their bodies, and if so whether or not they transferred viable spores from their bodies to the surrounding environment.

**MATERIALS AND METHODS**

To assess whether the flies or beetles were carrying spores, 12 individuals of each insect were collected in the vicinity of infected florets of *F. arundinacea* during the time of honeydew production. To determine whether the flies were carrying spores

on their bodies and/or in their guts, four flies were selected and each placed in a separate sterile vial to which 1 ml of sterile distilled water was added and then shaken for 1 minute using a vortex shaker. The number of *C. purpurea* spores per ml of water was counted by using a hemacytometer. To assess whether spores were present in fly guts, the abdomens were pierced, contents were shaken for an additional minute, and the spores counted. Gut spore content was calculated as the difference in spore counts before and after piercing. The same procedure was used for beetles. Because no fungal spores were found on the first four beetles, the remaining eight were also surveyed.

Since spores were found on the first four flies, the remaining eight were used to determine whether or not the flies carried and deposited viable spores onto objects on which they landed. The eight live flies were kept in separate sterilized glass vials for twenty four hours where they walked about and defecated. After the removal of the flies, each vial was rinsed with one ml of sterile distilled water. The number of spores in the rinse water was counted by using a hemacytometer, and one drop of the rinse water was plated onto each of two potato dextrose agar plates to count resultant colonies. Voucher specimens of the beetle are deposited at the Florida State Collection of Arthropods, Gainesville.

#### RESULTS

None of the twelve beetles surveyed carried *C. purpurea* spores internally or externally. In contrast, of four flies, three carried spores of *C. purpurea* externally, and all carried spores internally. The four individuals had a mean of  $5.1 \times 10^5$  spores/ml ( $SD 4.1 \times 10^5$  range  $0-1.04 \times 10^6$ ) on their body, and  $9.1 \times 10^6$  spores/ml ( $SD 2.4 \times 10^6$ , range  $5.3 \times 10^6 - 1.24 \times 10^7$ ) in their gut.

When kept in vials, the flies deposited a mean of  $2.76 \times 10^6$  spores/ml on the vial walls ( $SD 2.75 \times 10^6$ , range  $0-8.0 \times 10^6$ ). Some of the deposited spores were viable. Plating of approximately 0.1 ml of the spore suspension on agar yielded a mean of 36.57 colonies/plate ( $SD 45.81$ , range 0–100). The number of spores/ml of solution was not correlated with the number of colonies that developed (Spearman's rank correlation:  $r = 0.19$   $P < 0.33$ ).

#### DISCUSSION

At Mountain Lake, the fly, *M. lupulina* may be a spore dispersal vector for *C. purpurea*, but the mycophagous beetle, *Acylomus* sp. was not. This is unusual since the beetles, but not flies, were breeding in the fungus and, presumably, might be more specific to the fungus than are the flies. The flies carried spores on their body, and in their gut, and transferred the spores to their surroundings. It seems likely that flies transmit spores to receptive grass stigmas by touching them with their bodies or by defecating on them. It was not unusual for some florets on the panicle to be producing honeydew at the same time that other florets on the same panicle were producing stigmas. I observed flies walking around on grass panicles which were producing honeydew and receptive stigmas at the same time. It is likely that the severity of infection on an individual panicle is caused by flies visiting diseased florets and moving spores to healthy florets on the same panicle. I also observed flies moving from diseased panicles to different healthy panicles with receptive stigmas. Flies are

probably moving spores from diseased plants to healthy plants by landing on them when searching for spore-filled honeydew in the diseased plant population.—*Kathleen M. Lemon, The Nature Conservancy, 1815 North Lynn St., Arlington, Virginia 22209.*

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Thanks to Carol Horvitz, David Janos, and Helen Alexander who made useful comments on the manuscript. D. A. Grimaldi identified the fly and M. C. Thomas identified the beetle. This work was supported by the Pratt Predoctoral Fellowship from Mountain Lake Biological Station, University of Virginia, and by the Jerry Curtis Plant Sciences Scholarship from the Department of Biology of the University of Miami.

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*J. New York Entomol. Soc.* 100(1):184, 1992

#### A NEW HOMONYM IN THE MEZIRINAE (HEMIPTERA: ARADIDAE)

In 1967 I established a new genus, *Argocoris* Kormilev, for a new described species, *Argocoris grossi* Kormilev, from Queensland, Australia (Kormilev, 1967, Rec. S. Austral. Mus. 15:519). I have been advised that *Argocoris* Kormilev, 1967, is a junior homonym of *Argocoris* Mayr, 1864, Hemiptera: Pentatomidae (Verh. Zool. Bot. Ges., Wien, 14:905) which was created for *Argocoris redtenbacheri* Mayr, 1864.

To rectify this homonym, I therefore now propose the replacement name of *Pseudargocoris* Kormilev, new generic name, for *Argocoris* Kormilev, 1967.—*Nicholas A. Kormilev, 211 Pasadena Avenue N., Apt. 312, St. Petersburg, Florida 33710.*

#### ACKNOWLEDGMENT

I thank Dr. R. C. Froeschner (Smithsonian Institution, Washington, D.C.) for bringing this situation to my attention.

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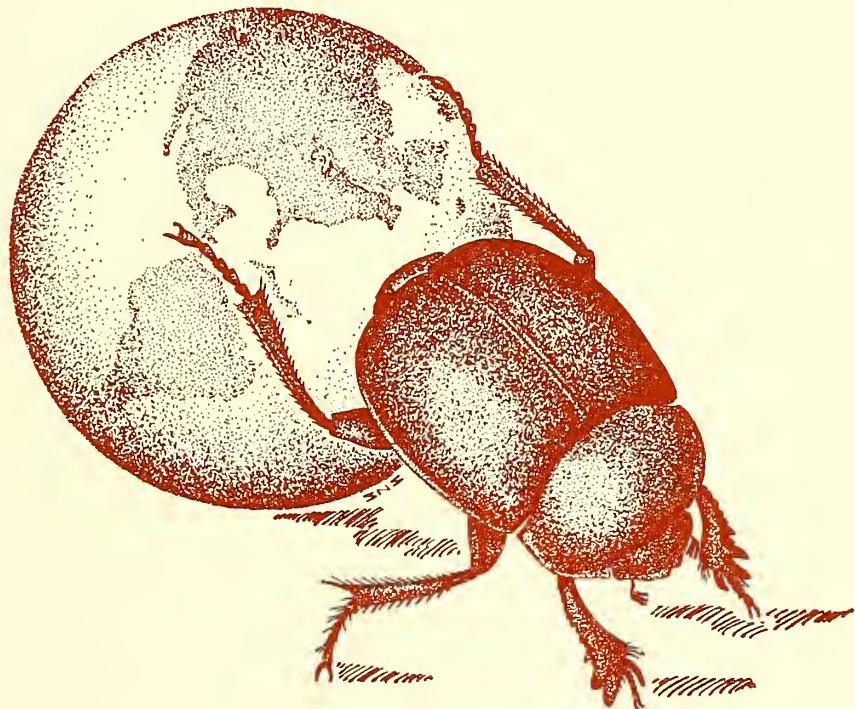
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**CONTRIBUTIONS FROM FORMER STUDENTS  
IN HONOR OF THE 80TH BIRTHDAY OF  
PROFESSOR JOHN G. FRANCLEMONT**

Organized by  
James K. Liebherr  
and  
E. Richard Hoebeke



John G. Franclemont, Angie and Duffy (NY: Tompkins Co., Ithaca, Snyder Heights, 13-X-1991, D. C. Ferguson).

## A REMEMBRANCE OF JOHN G. FRANCLEMONT

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John G. Franclemont, Jack to friends and colleagues, is a keen student of the Lepidoptera and a superb field naturalist. He was born on 15 April 1912 and raised in Buffalo, New York. He began collecting moths and butterflies at a very early age and was well instructed in the fine points of spreading specimens by an uncle. Summer vacations were spent on a farm where Jack's natural history interests and skills were further developed. Then, for several summers he was a nature counsellor at a Boy Scout camp in the Adirondack Mountains. By the time Jack entered Cornell University he knew that he wanted to become a specialist in the Lepidoptera, but he studied broadly and became well grounded in history, literature, and natural history generally with special emphasis on insects, plants, birds, and mammals. Soon, he met professor William T. M. Forbes, then the dean of Lepidopterists in North America, and the two became close associates. Jack Franclemont, Karl Krombein (also from Buffalo and now a Senior Scientist of the Department of Entomology, Smithsonian Institution), Laurence Rupert (a high school mathematics teacher in Horseheads, NY), and Ross Arnett were close friends during his undergraduate years. Many of Jack's fellow students also have became well-known entomologists including Ross Arnett, Jr., John Belkin, William Bodenstein, Eugene Gerberg, Karl Krombein, Woodrow Middlekauff, Eugene Munroe, L. L. Pechuman, Harvey Scudder, and Henry Townes. He received a BS degree in 1935 and was awarded the Ph.D. degree in 1953, both from Cornell University.

When WWII broke out, Jack entered the Army Medical Corps as an enlisted man. Subsequently, he went through officers' candidate school to become a commissioned officer. He served as a mosquito specialist in the Solomon Islands in the South Pacific and in the Philippines. Sometimes his unit arrived on islands while the Marines were still endeavoring to secure them. He collected intensively on Guadalcanal, Bougainville, New Georgia, and at Baguio in the Philippine Islands. He was moved westward from island to island and was stationed briefly in Japan at the end of the war. He was honorably discharged in San Francisco with the rank of Captain.

For a brief time Jack was an assistant entomologist (1946–47) at Cornell University. Then, he was an entomologist with the Bureau of Entomology and Plant Quarantine (the predecessor of the Systematic Entomology Laboratory), U.S. Department of Agriculture at the Smithsonian Institution from 1947 to 1953 where he was responsible for research, curation, and identification of noctuid and geometroid moths. In 1953 he became an associate professor of entomology at Cornell University, in 1959 full professor, and in 1982 emeritus. He continued to teach the advanced insect systematics course in Lepidoptera and to advise graduate students for several years after retirement.

During Jack's professional career he was the acknowledged authority on noctuoid moths of the Western Hemisphere. His extensive bibliography demonstrates the breadth of his interests, particularly the clarification of many difficult species-group problems and recognition of closely similar taxa.

His personal library was developed as a hobby and an investment. It has become one of the best privately held libraries in systematic entomology, and it is far superior to those in most universities. Naturally, the major emphasis is the Lepidoptera, but it is strong in several other areas. He was actively accumulating rare books and journals while many were still available and relatively affordable. It has been given to Cornell University, but he has lifetime use of it.

Building a personal collection of moths, particularly of the macrolepidoptera, has been a driving force during most of Jack's life. Although collecting the macrolepidoptera of the United States became a monumental endeavor, he never neglected the local fauna. This interest became ever more encompassing over the years and has resulted in the amassing of probably the finest collection of moths ever assembled through personal fieldwork, spreading, and curation. The level of quality in spread specimens and genital preparations set new standards, which, through his students, will influence North American museum collections well into the future. The material he provided for the teaching collection for the introductory insect systematics course was far more extensive and better prepared than the main collections of most universities, and typically was destroyed systematically by budding systematists. While he was a student and for the first few years in the 1950's he collected assiduously a locality on upper Six Mile Creek in the Ithaca watershed area, almost always accompanied by his dog. This area may be the best sampled locality for macrolepidoptera in the United States. He collected for several years at Arlington, Virginia and full summers in the following areas: Lakehurst, New Jersey; Highlands, North Carolina; Madera Canyon, Santa Rita Mountains (four years), Flagstaff (three years), and Chiricahua Mountains (three years), Arizona; and Big Timber, Montana. He has given most of his estimated 350,000 specimen collection to the Department of Entomology, Cornell University where it is well housed and readily accessible to workers. He gave the Pyraloidea and microlepidoptera to the National Museum of Natural History, Smithsonian Institution.

As well as collecting adults he has reared many broods of larvae. He established or verified hosts and preserved larvae of several hundred species. During collecting seasons one or more glass containers each with a single gravid adult female moth might be seen in his lab. Often viable eggs were laid to be followed with the provision of an array of suspected plant host leaves for the newly hatched larvae to try. The guessing game always began with knowledge of associated species' larval food plants. Success in finding an acceptable host plant was reasonably frequent, but the inclemency and relatively short growing season of the Ithaca area sometimes cut off the food supply before a brood had finished eating or the reverse when a southern species was captured on a spring field trip. Rearing larvae was a prominent part of all field work and often was one of the duties of a series of graduate student-field assistants. Many students have been field assistants and have gained immeasurably from their experiences.

Throughout his career Jack's interest in moths and many other insects, excellent memory, knowledge of the literature, true interest in students, and fine sense of

humor have served as a foil for many developing scientists. For most of his years at Cornell his schedule varied little: at the office shortly after eight, lunch in the office, dinner at home, then back to the office for the evening—an exception being the inevitable collecting on good evenings. The routine changed somewhat on Saturday and Sunday, but he was at the office even then. Any of his students and many others felt free to enter his office at any time to discuss a problem, seek advice, or talk. When a prominent visitor was in town, Jack usually arranged to have a social evening to which the graduate students and others were invited. Among many, I vividly remember one evening when Vladimir Nabokov was the guest. We students were and remain Jack's extended family. Among his Ph.D. students are George Ball (1954), Charles Triplehorn (1957), Donald Anderson (1958), Ronald Hodges (1961), Carroll Knowlton (1961), Feliciano Calora (1962), Donald Davis (1962), James Marshall (1964), Robert Dagleish (1967), Douglas Ferguson (1967), Jay Shaffer (1967), Robert Poole (1969), George Godfrey (1970), Ring Cardé (1971), David Furth (1976), Ali A. Ahmadi (1977), Timothy McCabe (1978), Frank Ramburg (1979), Richard Brown (1980), and John Rawlins (1982). Those for whom he chaired a master's degree committee or was a minor advisor for the doctoral degree are William Stockton, Mercedes Delfinado, Oliver Flint, Stuart Neff, Benjamin Foote, Lloyd Knutson, Albertus Bratt, Siu-Lam Lee, Thomas Pliske, Thomas Wood, Robert Dietz, Jay Abercrombie, Arthur Shapiro, Andre Comeau, Jorma Tahvanainen, Kuo-Ching Feng, John Burton, James Liebherr, Frank Slansky, Stanley Tuckwell, J. Mark Scriber, Ronald Kugler, Mark Lacey, Judith Abrams, Daniel Bickel, Stuart Krasnoff, and James Miller.

Jack was a true mentor to his students and thus provided guidance, challenges, and encouragement. He never expected them to agree with him but rather relished the differences and anticipated independence of thought. Much of his teaching and perhaps that for which he is best remembered was on a one-on-one basis. He worked best with self-motivated individuals. He effectively developed a sense of self confidence in his students that has helped them immensely. Because there was so much personal interaction between Jack and students, they have many cherished memories that illumine his personality. Above all, Jack is highly ethical, honest, positively forthright, helpful, humorous in a gentle, nondestructive way, and caring. All his students benefited from these qualities.

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NEOTROPICAL MICROLEPIDOPTERA XXV, A NEW  
ARBOREAL SPECIES OF *ACROLOPHUS* FROM  
PERU (LEPIDOPTERA: ACROLOPHIDAE)

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*Abstract.*—A new species, *Acrolophus arboreus*, of the endemic American family Acrolophidae is described from the upper Amazon of Peru. Similar larval material from Manaus, Brazil, suggests the species to be widespread through the Amazon Basin. The larvae are arboreal and construct elongate tubes of silk and wood fragments on the bark of several unrelated tree species. The larvae are believed to be scavengers on lichens and similar plant material.

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Little is known about the larval biology for the approximately 265 described species of the endemic American moth family Acrolophidae. Consequently, one can only speculate as to how diverse their life histories might be (Davis et al., 1986; Davis, 1987; Davis and Milstrey, 1988; Davis, 1990). It is generally believed that acrolophid larvae develop predominantly within a terrestrial habitat. The larvae of *Acrolophus*, for example, typically construct long silken, subterranean tubes amongst plant debris and roots upon which they feed (Hasbrouck, 1964). The few published records of arboreal *Acrolophus* refer to species living in the root system of epiphytic bromeliads (Picado, 1913; Beutelspacher, 1969).

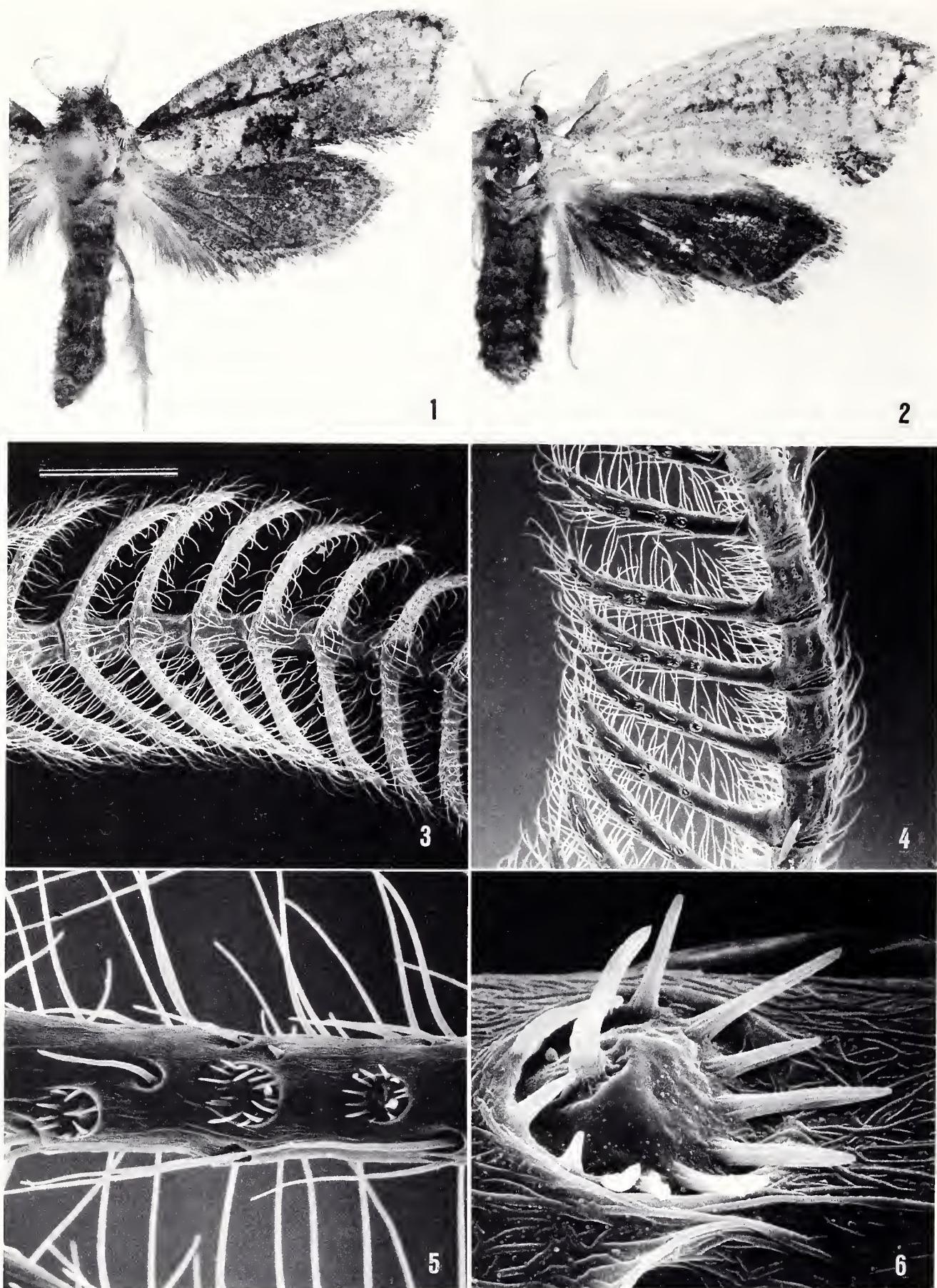
Field work over the past decade by the junior author (Hogue) has resulted in the discovery of an even “more arboreal” *Acrolophus*, whose larvae are believed to be scavengers on plant material growing on the bark of certain trees. A second arboreal and undescribed *Acrolophus* has also been observed in Costa Rica (D. Janzen, pers. comm.). A description of the Peruvian species is provided below.

Deposition of specimens referred to in this paper are: LACM for the Los Angeles County Museum of Natural History, Los Angeles, California and USNM for the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Abbreviations of morphological terms used for larval description defined in Davis, 1987.

***Acrolophus arboreus*, new species**

**ADULT** (Figs. 1, 2). Length of forewing: ♂ 12–13 mm; ♀, 12 mm. Moderately large moth with uniformly fuscous hindwings and variably marked dark fuscous to light brown forewings which are paler in the female. Labial palpi elongate in male, curving, over head to metanotum; much shorter and porrect in female.

**Head:** Vestiture short, slightly rough over middle (largely obscured by labial palpi in male); scales moderately slender to piliform with bidentate to acute apices, generally longer and more slender laterally along eye margin; fuscous with white scale



Figs. 1–6. Adult morphology, *Acrolophus arboreus*. 1. Male, length of forewing 11 mm. 2. Female, length of forewing 12 mm. 3. Basal third of male antenna, ventral view (200  $\mu\text{m}$ ). 4. Dorsal view of Figure 3 (150  $\mu\text{m}$ ). 5. Sensilla coeloconica enlarged from Figure 4 (27  $\mu\text{m}$ ). 6. Detail of single sensillum coeloconicum (5  $\mu\text{m}$ ). (Scale lengths in parentheses; bar scale for all photographs = Fig. 3.)

bases in male, mostly white in female. Eye relatively large; interocular index ca. 1.1 mm; cornea with dense covering of interfaceted setae, setae gradually becoming longer over posterior surface of eye; eyelash absent. Antenna short, less than 0.25 the length of forewing, 34–35 segmented; male with basal  $\frac{2}{3}$  strongly bipectinate (Figs. 3, 4); dorsal surface of rami densely covered with sensilla coeloconica (Figs. 5, 6), scape and pedicel fuscous irroriated with buff and dorsum of flagellum covered with dull white scales; female antenna simple with dorsum of basal  $\frac{2}{3}$  covered with scattered fuscous to brown scales, pedicel and scape white. Male with labial palpus elongate, curving over head to metanotum, fuscous laterally, pale buff to white mesally; labial palpus of female porrect, much shorter, ca. 1.5  $\times$  eye diameter, mostly light brown laterally, white mesally, with a prominent tuft projecting anteriorly from venter of second segment.

*Thorax:* Pronotum with dense mixture of short, moderately broad scales overlaid by elongate piliform scales, dull white irrorated with gray in male, mostly white irrorated with buff in female; venter densely covered with mostly white piliform scales. Forewing of male mostly light to medium fuscous with numerous fine, dark reticulate spots, a dark fuscous discal streak to base and a small rhomboidal anal spot; base of anal area distinctly lighter, mostly dull white; cilia brownish fuscous with a darker terminal line; forewing of female much lighter, light brown with darker brown reticulations and a much smaller, more slender brownish discal streak; sub-terminal area distinctly whiter. Hindwing uniformly fuscous in both sexes. Foreleg dark fuscous dorsally in male and dull white ventrally; light brown dorsally in female, white ventrally; epiphysis present, elongate, equal in length to foretibia. Midleg and hindleg progressively paler in both sexes; midtibia with dense brush of white piliform scales dorsally.

*Abdomen:* Almost entirely fuscous in male with caudal margins edged with white ventrally, especially over caudal three segments; generally paler in female, mostly light brown.

*Male genitalia:* As shown in Figures 35–38. Uncus moderately short, broad, and divided about half its length. Gnathos fused, mostly rounded with a slight, median cleft. Juxta absent. Valva broad, of complex outline, with a prominent, acute, apical lobe and an elongate, curved, acute saccular lobe closely associated with a membranous inner lobe from mesal membrane of valva. Aedoeagus elongate exceeding length of genital capsule, of complex form, with a broad median, uncinate cornutus and ca. 9 slender cornuti along apex of vesica.

*Female genitalia:* As shown in Figure 39. A single pair of short posterior apophyses present. Caudal margin of lamella antevaginalis irregularly serrate, well sclerotized. Ostium broad in diameter, width ca. equal to length of apophyses. Ductus bursae broad, short, sclerotized. Corpus bursae bilobed, relatively small, length only slightly exceeding that of ductus bursae; walls completely membranous.

**LARVA** (Figs. 10–34). Length of largest larva 32 mm; maximum diameter 3 mm. Body mostly gray dorsally over anterior half, lighter and predominantly cream to white over remainder of body; thoracic and anal plates and pinacula dark fuscous to gray.

*Head:* Dark reddish brown anteriorly, dark fuscous posteriorly. Maximum width 2 mm. AF2 arising at level of apex of frons. P2 more distant from P1 than P1 is to ecdysial line. Six pairs of stemmata present (Figs. 15, 28); 3–5 contiguous anteriorly



7



8



9



10

Figs. 7-10. Larval biology of *Acrolophus arboreus*. 7. Larval cases (see arrows) on tree trunk, Yanamono, Peru. 8. Underside view of chambered node of larval tube. 9. Larval tube, length ca. 35 cm (scale = 2 cm). 10. Larva, length ca. 30 mm.

between S1 and SS1; 6 reduced. Antennal sensilla as shown in Figures 29, 30, similar to that of *Acrolophus pholeter* Davis (1988) except segment 4 lacking apical extension. Labrum similar to *A. pholeter*. Mandible with 2 distinct cusps and two much reduced cusps; lateral (first) cusp elongate, acute (Fig. 18). Maxilla as shown in Figures 25–26; all sensilla basiconica (3 + 3 + 2) shorter than those of *A. pholeter*; A2 styloconic; sensillum digitiformium (SD) greatly reduced, subapical. Spinneret and labial palpus (Figs. 20, 24) similar to *A. pholeter*. Apex of mentum with a pair of minute secondary setae (Fig. 22).

**Thorax:** Pronotal and mesonotal plates dark reddish brown to nearly black. Spiracular plate almost completely separated from pronotal plate by a narrow fissure; all 3 lateral setae together on spiracular plate. Coxal plates narrowly separated (Fig. 31). Tarsal claw (Fig. 32) with minute, slender axillary seta.

**Abdomen:** A1–6 with 11 pairs of primary setae, SV trisetose. A7–8 with SV3 absent. A9 with 9 setal pairs, SV unisetose. Ventral crochets in a uniserial ellipse of approximately 50–53 hooks; anterior and posterior sides of prolegs densely covered with small scattered spines, more numerous anteriorly. Anal proleg with ca. 28 hooks in a half ellipse open posteriorly and covered with dense spines anteriorly. A8 with spiracle greatly enlarged, equalling size of prothoracic spiracle. Anal plate with 4 pairs of elongate setae.

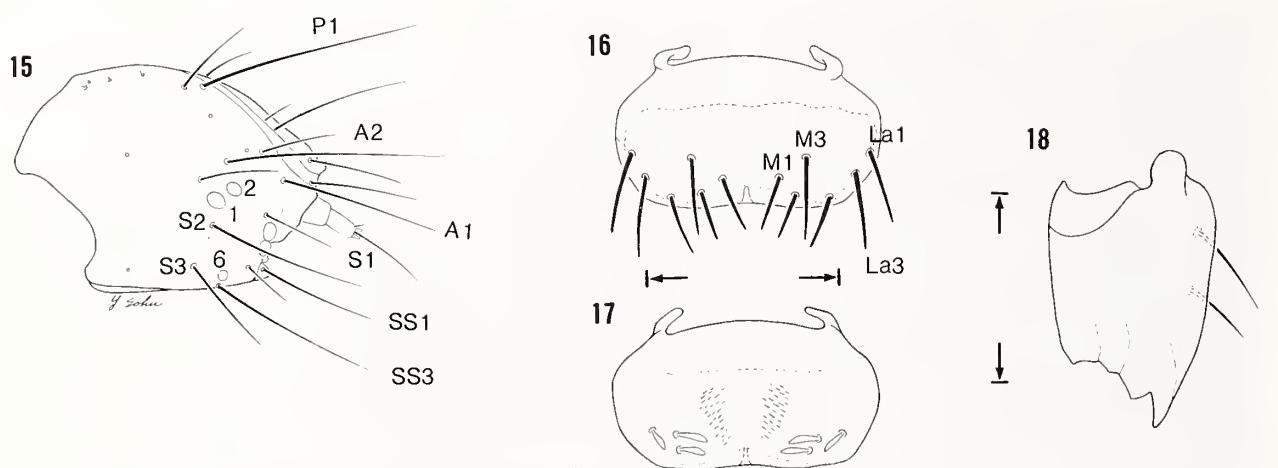
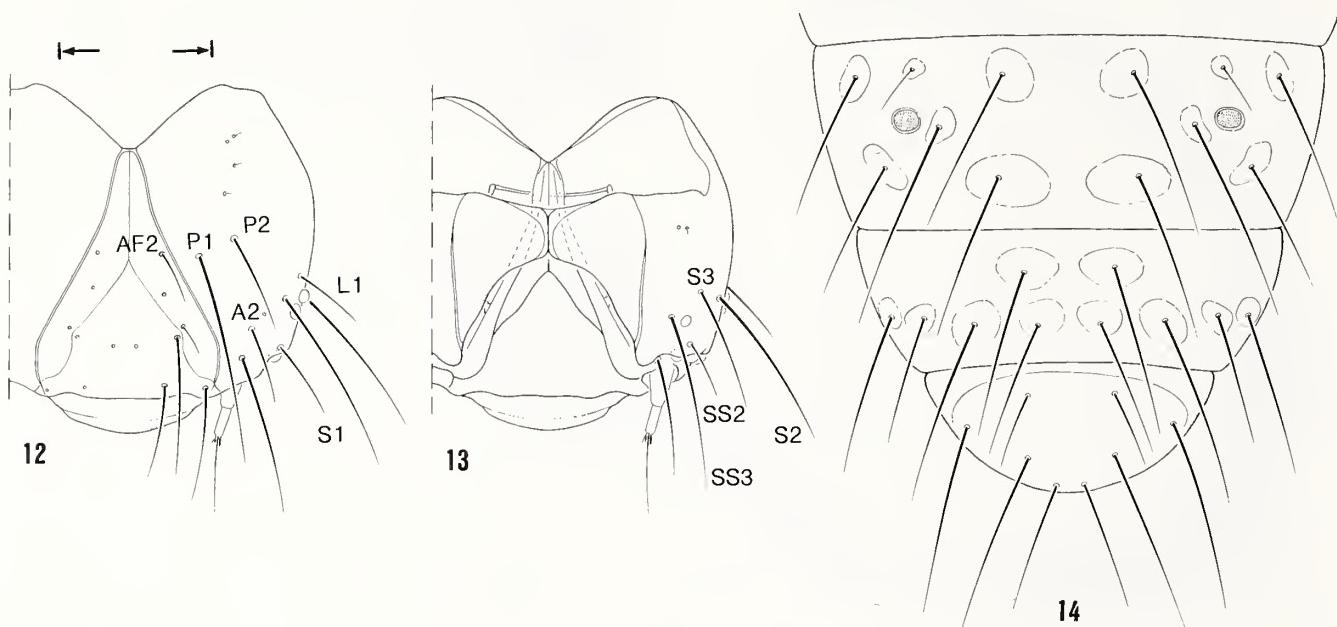
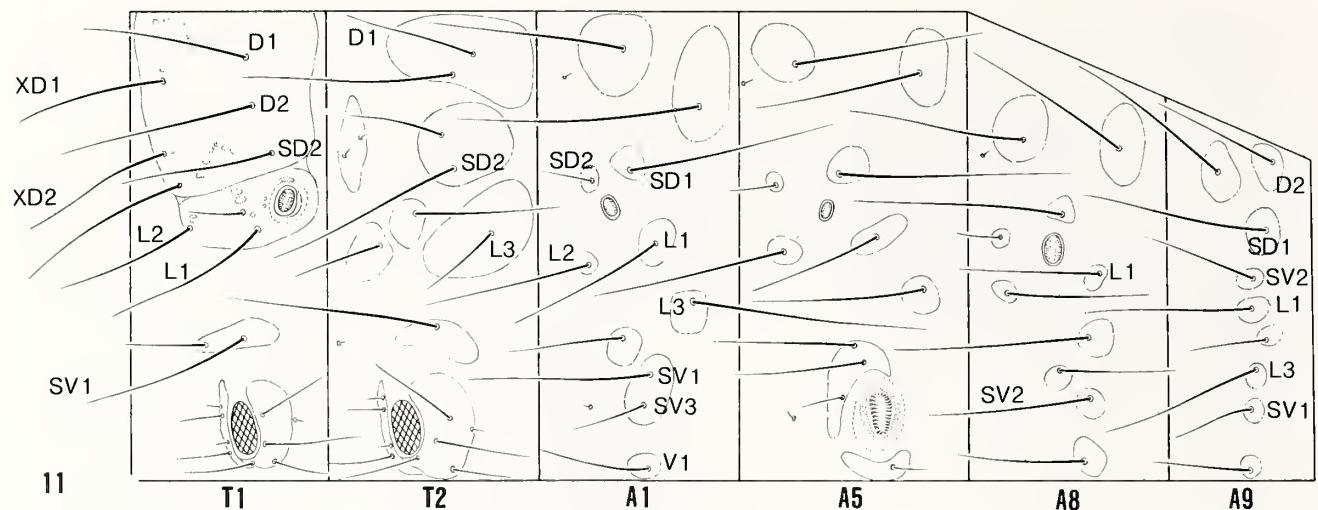
**LARVAL CASE** (Figs. 7–9). An elongate tube up to 35 cm in length and 5 mm in diameter, constructed of minute wood fragments held together by silk; a 3 to 6 chambered, oval, abruptly enlarged dome-like section variably situated somewhere along midlength of tube, up to 40 mm long, 30 mm wide and 15 mm high. Inner surfaces of larval tube and chamber smoothly lined with thin layer of whitish silk; cavity devoid of frass or debris. Larval tube extends through chamber intact, without any openings; partitions of central chamber possibly due to successive enlargement of chamber. Color light to dark brown.

**PUPA** (Figs. 40–48). Length of largest pupa: ♂, 12 mm; ♀, 12.8 mm. Dark reddish brown in color. Vertex smooth except for a pair of small setae near middorsal line. Frons with a small pair of setae near inner margin of eye (Figs. 40, 41, 44). Antenna of male relatively longer and much broader than in female; labial palpus ca. twice as long in male than female. Wings extend to middle of A3. Mesonotum with two pairs of dorsal setae, D1 more anterior and separated further apart than D2. Dorsum of A3–8 with a low, transverse, minutely and densely spined (Figs. 45, 46) ridge parallel to anterior margin. A10 a relatively small, acutely furcate cremaster dorsally (Figs. 47, 48).

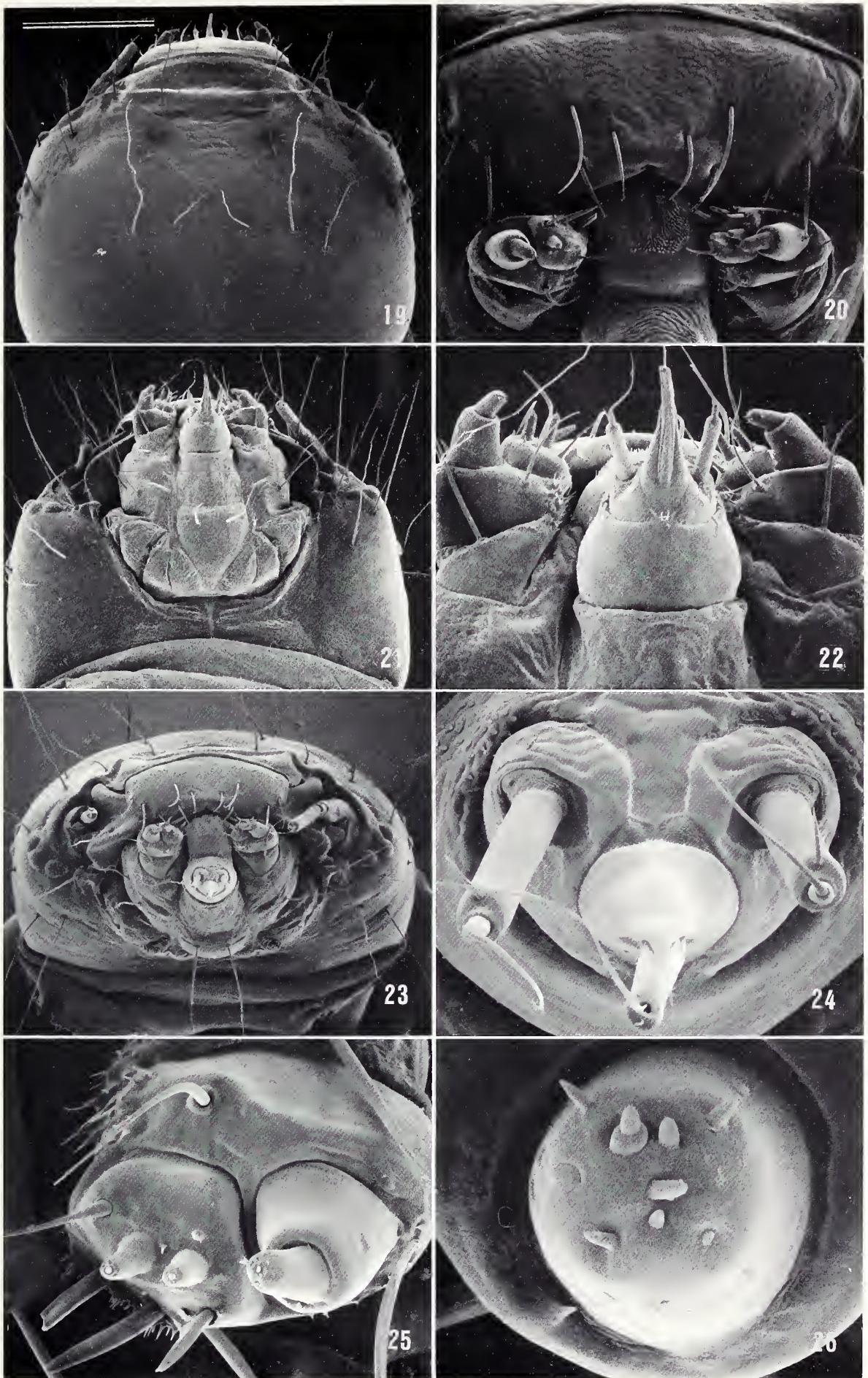
**HOLOTYPE.** ♂, Yanamono, 80 km east of Iquitos, Loreto Department, Peru; 3 Jul 1990, emerged 28 Jul 1990, C. L. Hogue (LACM).

**PARATYPES.** PERU. Loreto Department: Amazon Safari Camp, Río Momon, near Iquitos: 1 ♀, 25 Jun 1980, emerged 12 Aug 1980, C. Hogue, CLH 268.1, genitalia slide 3669 (LACM); 1 ♂ pupa, 25 Jun 1980 (LACM). Yanamono, 80 km E Iquitos: 1 ♂, emerged Jul 1982, C. Hogue (LACM); 1 ♂, emerged 20 Jul 1983, pupal slide 3653–54 (LACM); 1 ♂, emerged 23 Jul 1983, C. Hogue (LACM); 1 ♂, emerged 23 Jul 1983, antenna slide 28638 (USNM); 1 ♂, emerged 28 Jul 1983, genitalia slide 30926, C. Hogue (USNM). Same data as holotype, 1 ♂ (LACM); 20 larvae, 3 Jul 1990, C. Hogue slides 30696–98 (USNM, LACM).

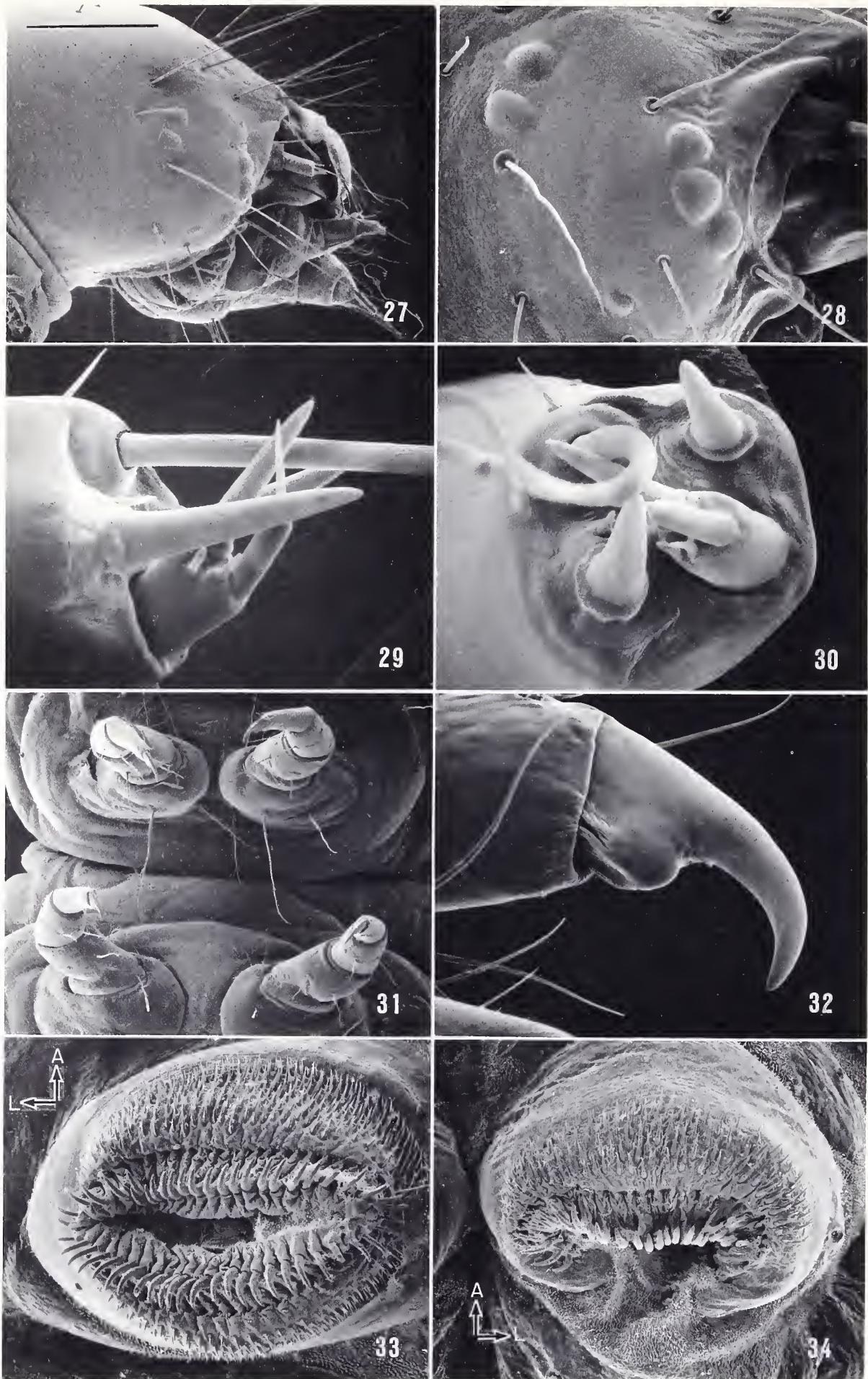
**HOST.** Unknown; most probably various lichens and other plant debris on the



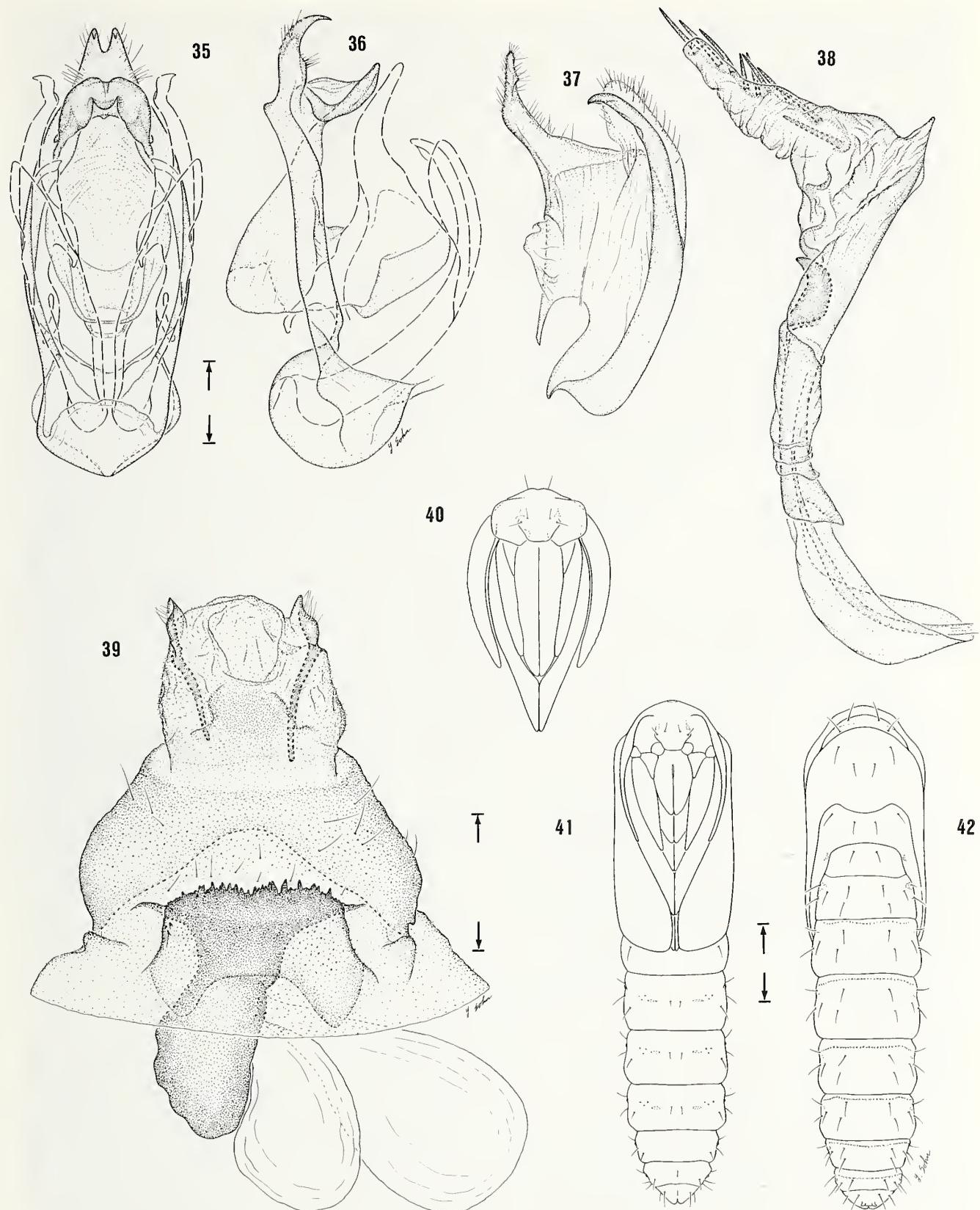
Figs. 11-18. *Acrolophus arboreus*, larval morphology. 11. Chaetotaxy of pro- and mesothorax, abdominal segments, 1, 5, 8, 9. 12. Head, dorsal view (0.5 mm). 13. Head, ventral view. 14. Abdominal segments 8-10, dorsal. 15. Head, lateral view. 16. Labrum, dorsal (0.5 mm). 17. Labrum, ventral. 18. Mandible (0.5 mm). (Scale lengths in parentheses.)



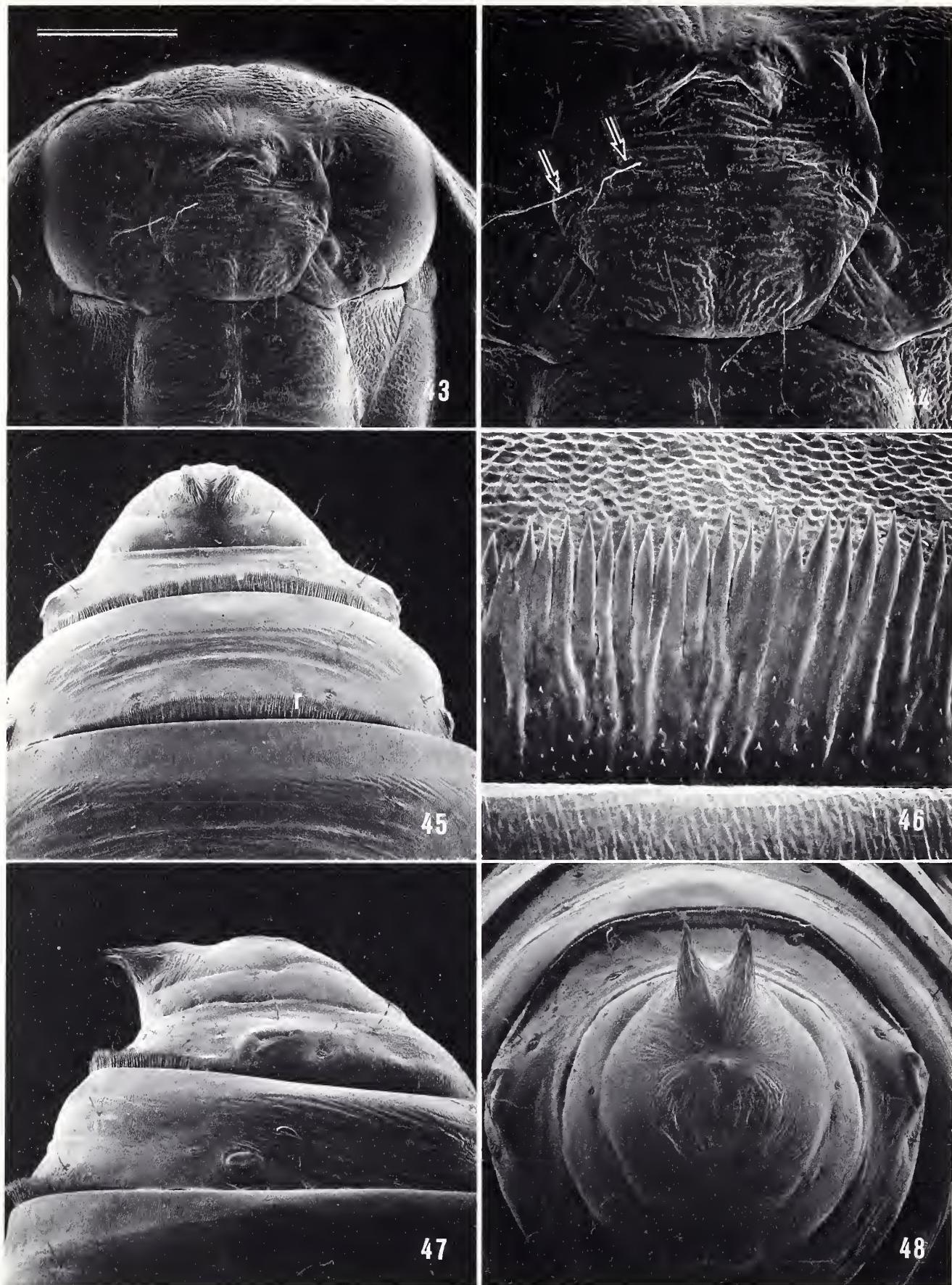
Figs. 19–26. *Acrolophus arboreus*, larval morphology. 19. Head, dorsal view (0.6 mm). 20. Labrum and maxilla (231  $\mu\text{m}$ ). 21. Head, ventral view (0.6 mm). 22. Labium and maxilla, ventral view (200  $\mu\text{m}$ ). 23. Head, anterior view (0.6 mm). 24. Labial palpi and spinneret (60  $\mu\text{m}$ ). 25. Maxilla (75  $\mu\text{m}$ ). 26. Sensilla of maxillary palpus (15  $\mu\text{m}$ ). (Scale lengths in parentheses; bar scale for all photographs = Fig. 19.)



Figs. 27–34. *Acrolophus arboreus*, larval morphology. 27. Head, lateral view (0.5 mm). 28. Stemmatal area (231  $\mu\text{m}$ ). 29. Antenna, lateral view (23.1  $\mu\text{m}$ ). 30. Antenna, distal view (23.1  $\mu\text{m}$ ). 31. Thorax, ventral view of T1 and 2 (0.67 mm). 32. Pretarsus, lateral view of T1 (50  $\mu\text{m}$ ). 33. Abdominal proleg, A3 (150  $\mu\text{m}$ , A = anterior, L = lateral). 34. Anal proleg (150  $\mu\text{m}$ ). (Scale lengths in parentheses; bar scale for all photographs = Fig. 27.)



Figs. 35–42. *Acrolophus arboreus*, genital morphology and pupae. 35. Male genitalia, ventral view (0.5 mm). 36. Lateral view. 37. Valva, mesal view. 38. Aedoeagus. 39. Female genitalia, ventral view (0.5 mm). 40. Male pupa, head. 41. Female pupae, ventral view (0.5 mm). 42. Dorsal view of Figure 41. (Scale lengths in parentheses.)



Figs. 43–48. *Acrolophus arboreus*, pupal morphology. 43. Head, ventral view (0.6 mm). 44. Frons, with paired setae (see arrows) (0.33 mm). 45. Dorsal view of A6–10 (0.6 mm). 46. Detail of serrated dorsal ridge of A7 (see r in Fig. 45) (60  $\mu$ m). 47. Lateral view of A6–10 (0.6 mm). 48. Caudal view of A10 (0.6 mm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 43.)

bark of several trees including *Chimarrhis glabriflora* Ducke (Rubiaceae) and *Ficus insipida* Willd. (Moraceae).

**FLIGHT PERIOD.** June–August. Because collecting was conducted only during this period, which occurs in the middle of the dry season, the maximum flight period and seasonality of this species are uncertain.

**DISTRIBUTION.** Adults known only from type locality, an area in the Peruvian Amazon in the vicinity of Explorama Lodge (=Yanamono), ca. 80 km E Iquitos, Department of Loreto. Perhaps widely distributed in the Amazon Basin as indicated by larval cases observed in Manaus, Brazil (see ethnological note).

**ETYMOLOGY.** The specific name is derived from the Latin *arboreus* (of trees) in reference to the unusual, arboreal habit of the larva.

**TAXONOMIC DISCUSSION.** Currently, *Acrolophus arboreus* does not appear closely related to any described species in this large genus. The unusual structure of the male genitalia, particularly the rather complex form of the valva and thickened gnathos, show no close affinities to a similarly arboreal and undescribed *Acrolophus* from Costa Rica.

Larval chaetotaxy appears to be very conservative within *Acrolophus*. Possibly the reduced sixth stemma is the most diagnostic larval character for this species. Among the few known larval cases, the swollen, centrally located chamber is unique. The similar case observed in Manaus, Brazil (see ethnological note) probably represents this species.

**BIOLOGICAL OBSERVATIONS.** Larval tubes have been observed on the trunks of several tree species, including two identified by A. Gentry (pers. comm., letter of 31 Aug. 1982 to Hogue) as *Chimarrhis glabriflora* Ducke and *Ficus insipida* Willd. The tubes are located from 3 to 7 m above the ground and normally oriented vertically. They are easy to see, usually being of slightly different color than the tree bark. The tubes are weakly attached to the bark surface along their entire length but adhere more tightly at the upper end, their apparent origin.

The function of the chambered, swollen node located along the middle of the larval tube was not observed. Possibly the larva uses this as a retreat even though no openings in the tube were observed within the cup-like chamber. An outer shell around the tube might provide some added protection. Likewise, larval feeding was not observed. Possibly the larva gleans lichens or other plant material from either end of the tube.

**ETHNOLOGICAL NOTE.** During a visit to the Municipal Market in Manaus, Brazil, on 25 April 1990, Hogue noticed the larval tubes of *A. arboreus* (or a very close relative) in a stall where basketry and sundries were sold. Hogue was told by the vendor that the tubes were called (in Portuguese) "rede de tamaquaré," meaning "net of the tamaquaré lizard." He believed that this lizard, which is frequently found climbing on tree trunks in the nearby forest, was responsible for making the tubes.

The tubes were described by the vendor as useful in "black magic," to influence the humor of one's spouse or sweetheart, as follows: "Colocar o nome dentro da rede, e colocar embaixo do traveseiro." Put the name [of one's lover, on a piece of paper] inside the net and place it under [her] pillow. In the morning she will wake up in a perfectly friendly mood.

The common name "tamaquaré" (syn. "taquaré") in Brazil applies to *Enyalia* spp. (von Ihering 1968:675). A poorly preserved specimen of the alleged net maker shown

to Hogue by the vendor appeared not to be of this genus but the very common, often arboreal, *Tropidurus torquatus* Van Lidth de Jeude, 1917, known in Brazil as "tarraquirá." In any case, identification of the lizard is unimportant to the story, the locals being imprecise taxonomists.

#### ACKNOWLEDGMENTS

We wish foremost to express our gratitude to John G. Franclemont for the very competent advice and assistance which he generously provided over the years and to congratulate him for the numerous accomplishments he achieved throughout his distinguished career, both as entomologist and teacher. We are indebted to Young Sohn of the Department of Entomology, National Museum of Natural History, for the line drawings and to Susann Braden and Walt Brown of the Smithsonian SEM Lab and Victor Kranz of the Smithsonian Office of Photographic Services for photographic assistance. Acknowledgment is made to the University of California at Los Angeles Extension and Society Expeditions, Seattle, Washington, for financing the trips on which the material was collected. Thanks also to Tina Ross for preparing the final draft of the manuscript.

The senior author (Davis) is responsible for the systematic and morphological portions of this paper and the biological and ethnological observations are by the junior author (Hogue) who discovered the species. This report constitutes contribution XXV in the Smithsonian Neotropical Microlepidoptera series.

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## TWO NEW SPECIES OF *MOMPHA* FROM CALIFORNIA (LEPIDOPTERA: MOMPHIDAE)

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*Abstract.*—Two new species of *Mompha*, *franclemonti* and *powelli*, from California are described to provide names that support long-term biodiversity studies of natural areas in California. *M. powelli* was reared from *Zauschneria californica* (Onagraceae).

Specimens of an undescribed species of *Mompha* were collected during a long-term survey of Lepidoptera of Big Creek Reserve, Monterey County (one of the University of California's natural land reserves) by Jerry A. Powell (UC Berkeley). Subsequently, a closely similar, but slightly smaller species of *Mompha* was collected in the hills immediately east of San Leandro, Alameda County. The second species later was reared from *Zauschneria californica* Presl, Onagraceae. To make a name available for his planned report and to document some of the diversity within *Mompha* both species are described.

The new species are black marked with white and are most similar to *Mompha metallifera* (Walsingham). In the National Museum of Natural History's (USNM) insect collection several, mainly eastern, specimens also are very similar to *metallifera*, including a series reared from *Cuphea viscosissima* Jacquin, Lythraceae (as *C. petiolata*) by Annette F. Braun and incorrectly determined as *metallifera*. This species proved to be undescribed. I have not found any other male specimen whose genitalia match those of the holotype of *metallifera*. After dissecting males (females are not well represented) of most of the miscellaneous specimens, I find that no less than 12 species are present. Only three of them have names: *metallifera*, *argentimaculella* (Murtfeldt), and *annulata* (Braun). Careful study of color pattern leads me to believe that separation of these species on this basis may be impossible or extremely difficult. Sexual dichromatism occurs in the series reared by Braun: males have the distal  $\frac{1}{2}$  of the antenna uniformly black; females have the distal three segments white preceded by black segments.

My initial intent was to analyze these similar-appearing species, prepare an identification key, and illustrate the genitalia of each entity. This proved to be too large a project for the present purpose and thus is deferred until a thorough study can be made of nearctic *Mompha*. My preliminary study of this genus leads me to suspect that the fauna may be more than 100 species and have several cryptic species' complexes.

### ***Mompha franclemonti*, new species**

Figs. 1, 3, 5

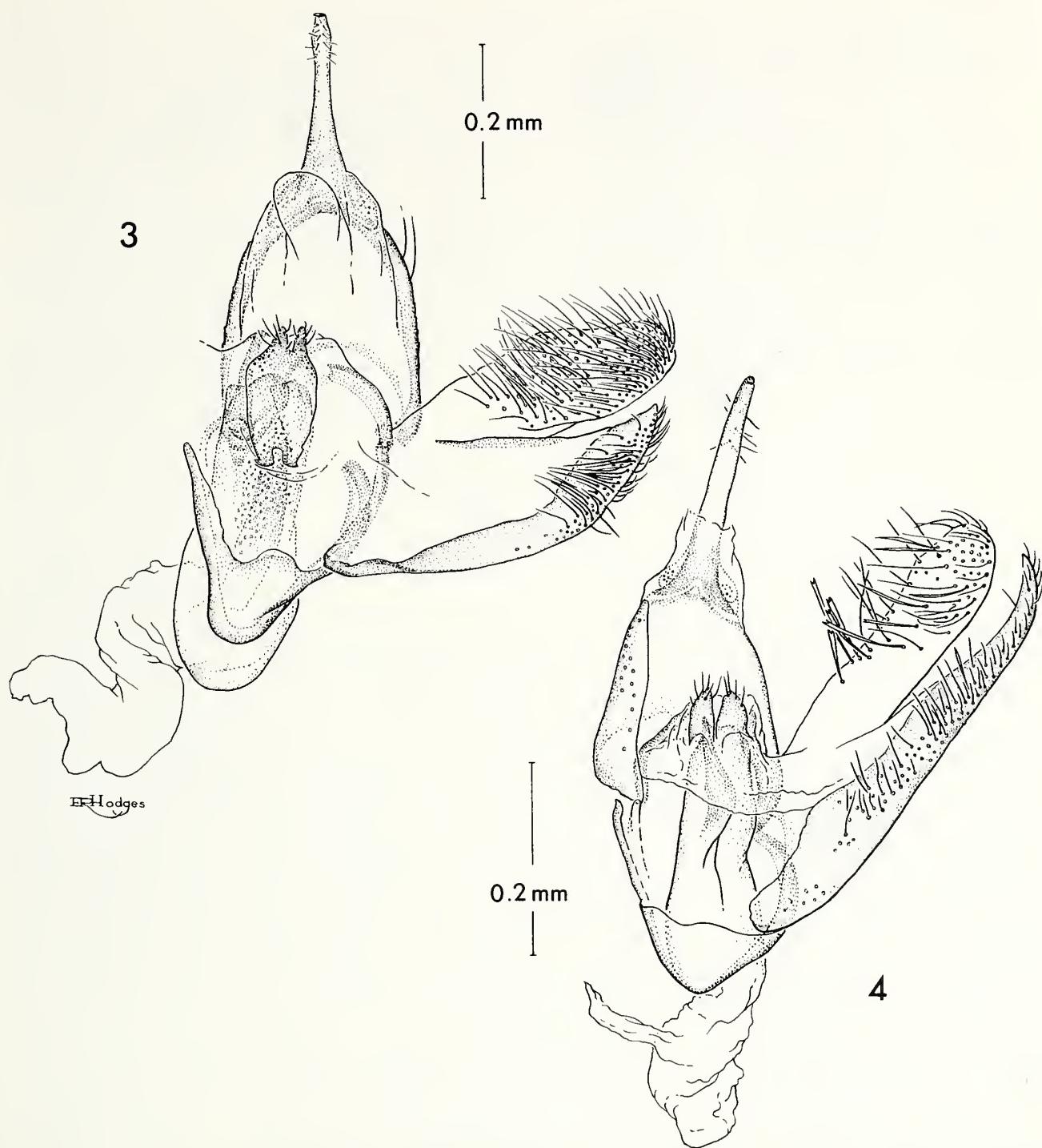
*Diagnosis.* A superficially very dark-gray moth having shining silver transverse fasciae, one at  $\frac{2}{5}$ ,  $\frac{4}{5}$ , and  $\frac{5}{6}$  forewing length. All surfaces, except ventral surface of



Figs. 1-2. Photographs of *Mompha* species. 1. *M. franclemonti*, n. sp., holotype ♂. 2. *M. powelli*, n. sp., holotype ♂.

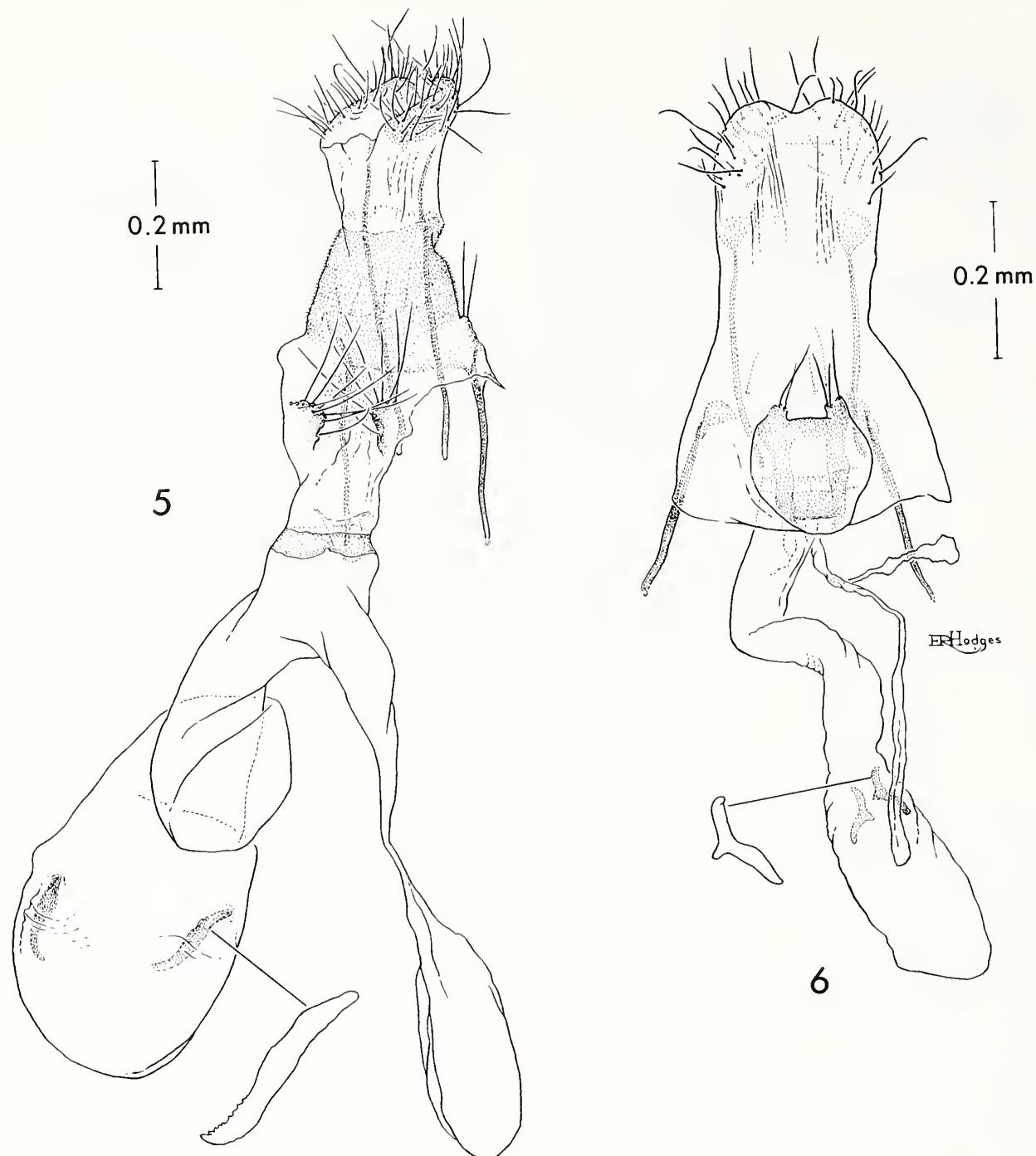
fore- and hindwings and white areas, with shining reflections, usually mainly silvery but sometimes with yellow or yellow-gray cast. *Mompha franclemonti* is most similar to *M. powelli* but differs as follows: 1) The mesial surface of the labial palpus is paler than the lateral surface and the pale-gray tipped scales are less contrasting on the mesial surface than the lateral surface (*franclemonti*); the mesial and lateral surface of the labial palpus are similarly shaded and hued, and the pale-gray to off-white areas of the scales are large (*powelli*). 2) The forewing has many, small white dots (*franclemonti*); the forewing lacks white dots (*powelli*). 3) The aedoeagus has a nearly parallel-margined, very broadly rounded cornutus and a sclerotized band with tooth-like projections (*franclemonti*); the lateral margins of the cornutus taper within the distal  $\frac{1}{2}$  to a slender, rounded apex (*powelli*). 4) The distal lobes of the juxta are separated mesially by a U-shaped area and appear like a pair of nipples (*franclemonti*); the distal lobes of the juxta are separated by a very narrow, V-shaped area, are broad basally and taper laterally within the distal  $\frac{1}{3}$  to a rounded apex (*powelli*).

*Description.* Head: Haustellum very dark gray with a few pale-gray tipped scales basally, becoming naked and yellowish distally. Labial palpus medium gray mesially, dark gray laterally, many scales tipped with pale gray on second segment and off-white on third segment. Frons nearly black with shining metallic silver reflections; vertex and occiput dark gray with shining metallic silver reflections; scales behind eye nearly black. Antenna very dark gray, distal segment gray preceded by  $1\frac{1}{2}$  very dark-gray segments (more pronounced on ventral surface), then somewhat irregularly alternate  $\frac{1}{2}$  segments gray and very dark gray. Thorax: Tegula very dark gray basally, gray distally; meso- and metathorax very dark gray. Foreleg mainly very dark gray becoming darker distally, apex of tibia with a few slightly paler scales, apexes of first



Figs. 3-4. Male genitalia of *Mompha* species. 3. *M. franclemonti*, n. sp., paratype, USNM genitalia slide 86613. 4. *M. powelli*, n. sp., paratype, USNM genitalia slide 86611.

four tarsomeres white, apex of fifth tarsomere gray. Midleg as for foreleg but tibia with a faint, gray transverse fascia at  $\frac{1}{2}$  length and prominently white at apex. Hindleg as for midleg but with prominent, transverse, white fascia at  $\frac{1}{2}$  length and spurs mainly white with some gray areas. Forewing mainly very dark gray with prominent salt-and-pepper pattern caused by a small white area just before the apex of many individual scales or at the apex of scales on the distal part of the wing; a patch of raised scales on the fold at  $\frac{1}{2}$  wing length and one on the posterior  $\frac{1}{2}$  of the wing just beyond  $\frac{4}{5}$  wing length, a diffuse zone of silver-colored scales at base of wing, a silver, transverse fascia at  $\frac{2}{5}$  wing length, another at  $\frac{4}{5}$  wing length, and a curved



Figs. 5–6. Female genitalia of *Mompha* species. 5. *M. franclemonti*, n. sp., paratype, USNM genitalia slide 15992. 6. *M. powelli*, n. sp., paratype, USNM genitalia slide 86612.

silver band on the outer margin of the wing; fringe at apex of wing gray preceded by a narrow black line, then white dots, then a black area with scattered white dots, fringe in tornal area medium to pale gray; undersurface different shades of gray; length 3.0–4.0 mm. Hindwing medium to pale gray on dorsal and ventral surfaces. Abdomen: dorsal surface mainly very dark gray, prominently shining silvery gray laterally and on posterior margin of several segments, mesial parts of terga 3–5 with yellowish gray to orange gray; ventral surface very dark gray, apex of sterna broadly shining white or silver white, eighth sternum mainly dark with a few white scales mesially. Male genitalia (Fig. 3): anterior margin of costal lobe of valva arising from base of valva, continuing as heavily sclerotized transtilla, maximum width of costal

lobe  $0.75 \times$  width of valva at base; transtilla incomplete, not meeting mesially; aedeagus with very broad, distal cornutus that is broadly rounded distally and with a diffuse sclerotized band bearing many denticular projections; juxta with pair of short lobes distally. Female genitalia (Fig. 5).

**Etymology.** Named in honor of my long-time friend and mentor, John G. Franclemont.

**Holotype.** ♂, USA. California: Monterey Co.: Big Creek Reserve, UCNLWRS, mining ridge, 80–180 m, sage chapparal, 21/23 III 1989, F. Hsu, J. Powell; deposited in the University of California, Berkeley, Entomology Museum.

**Paratypes.** Same data as holotype, USNM genital slides 15991, 15992, 86613, RW Hodges slide 5140, 13 ♂♂, 2 ♀♀ (UCB, USNM). Same locality as holotype, 21/22 II 1988, J. A. Powell, 1 ♂ (UCB).

### **Mompha powelli, new species**

Figs. 2, 4, 6

**Diagnosis.** Superficially, *powelli* is similar to *franclemonti* but differs as indicated under *franclemonti*.

**Description.** Head: Haustellum shining pale gray becoming yellowish gray distally. Labial palpus medium gray, most scales of second and third segments broadly tipped with pale gray. Frons and vertex shining silver gray, occiput very dark gray with shining yellow reflections, row of scales behind eye very dark gray to shining gray. Antenna very dark gray, most scale bases slightly paler than apices. Thorax: Tegula, meso- and metathorax very dark gray. Foreleg mainly very dark gray; coxa prominently shining silver gray; apexes of many scales on femur and tibia pale gray, apex of epiphysis with a few off-white scales and apex of tibia white; apex of tarsomeres one, two, and four white. Mid- and hindlegs much as for foreleg but scales of femur and tibia without pale apexes, tibia with a prominent white fascia at  $\frac{3}{5}$  length. Forewing mainly very dark gray, scale bases often slightly paler gray, a diffuse zone of translucent silver-colored scales at base, a prominent shining silver fascia at  $\frac{2}{5}$  length and one at  $\frac{3}{4}$  length, a shining silver spot on posterior margin at  $\frac{1}{2}$  length, a few silver scales on anterior margin at  $\frac{1}{2}$  length, and a band of shining silver scales paralleling distal margin; a patch of raised scales on the fold at  $\frac{1}{2}$  the wing length and another on the posterior margin at  $\frac{3}{5}$  length; a few pale-gray tipped scales on posterior  $\frac{1}{3}$  of wing before first silver fascia; fringe at apex of wing gray preceded by a narrow black line, then white dots, then a black area with scattered white dots, fringe in tornal area medium to pale gray; undersurface mainly medium to pale gray; length 2.7–3.7 mm. Hindwing medium to pale gray on dorsal and ventral surfaces. Abdomen: as for *franclemonti*. Male genitalia (Fig. 4): anterior margin of costal lobe of valva arising from base of valva, continuing as heavily sclerotized transtilla, maximum width of costal lobe approximately  $0.50 \times$  width of valva at base; transtilla incomplete, not meeting mesially; aedeagus with large distal cornutus, lateral margins tapering within distal  $\frac{1}{2}$  to slender, rounded apex; lobes of juxta broad, mesial margins slightly diverging, lateral margins angled mesially at  $\frac{1}{2}$  length to rounded apex. Female genitalia (Fig. 6).

**Etymology.** Named in honor of the collector and colleague, Jerry A. Powell.

**Holotype.** ♂, USA. California: Alameda Co.: Fairmont Ridge, SE of San Leandro,

3 V 1989, J. Powell; J. Powell No. 89E6, emgd. 28 v 1989, reared from *Zauschneria calif.[ornica]*; deposited in the University of California, Berkeley, Entomology Museum.

*Paratypes.* Same data as holotype but emerged 24–29 V 1989, USNM genitalia slide 15990, 4 ♂♂, 4 ♀♀. Same locality as holotype, 19 iv 1989, J. Powell; J. Powell No. 89D33, emgd. 9–22 V 1989, reared from *Zauschneria calif.[ornica]*, USNM genitalia slides 15989, 86611, 86612, 5 ♂♂, 4 ♀♀. Same locality as holotype, 3 V 1989, 31 VIII 1989, J. Powell, 10 ♂♂, 6 ♀♀ (UCB, USNM).

*Distribution.* An additional specimen of *powelli* was collected at Whittier, Los Angeles Co., California on 4 III 1911 by P. H. Timberlake. It is not included in the type series, but study of the male genitalia (USNM genitalia slide 5324) shows it to be conspecific.

#### ACKNOWLEDGMENTS

I thank Jerry A. Powell (University of California, Berkeley; UCB) for allowing me to study material collected by him; my wife, Elaine R. S. Hodges, for the line drawings of genitalia; Douglas C. Ferguson for the photographic prints and review of the manuscript; and Don R. Davis, Richard C. Froeschner, and Arnold S. Menke for review of the manuscript.

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## SIX NEW SPECIES OF *CATASTEGA* (LEPIDOPTERA: TORTRICIDAE: EUOSMINI) FROM MEXICO AND SOUTHWESTERN UNITED STATES

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*Abstract.*—In celebration of the eightieth birthday of Dr. John G. Franclemont, six new species of *Catastega* (Lepidoptera: Olethreutinae: Eucosmini) are described as follows: *C. spectra*, from Texas, *C. nebula*, from Arizona, *C. strigatella*, from New Mexico, Texas, and Mexico, *C. triangulana*, from Arizona and Mexico, *C. adobe*, from Arizona, New Mexico, and Texas, and *C. plicata*, from Arizona and Mexico.

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This paper is dedicated to Dr. John G. Franclemont, because of his direct and indirect contributions in documenting the Lepidoptera fauna of the southwestern United States. Dr. Franclemont, assisted by a number of graduate students, spent a total of 31 months in Arizona during nine extended periods between 1959 and 1974; these field trips were notable for the intense collecting, e.g., 99 nights out of a possible 100 in 1960, and the resulting large number of undescribed taxa that were collected (Franclemont, 1961, 1964, 1976). During these trips to Arizona, Dr. Franclemont collected several species of Olethreutinae in various genera that remain undescribed, and his graduate students collected three of the following six new species of *Catastega* Clemens. Species of *Catastega* from Texas, New Mexico, and Mexico similar to those in Arizona also are treated here.

The North American genus *Catastega* was resurrected from synonymy with *Epinotia* Hübner and characterized by apomorphies of the male anellus and female sterigma by Brown (1986). At present the genus includes two eastern species, *C. timidella* Clemens and *C. aceriella* Clemens, which have larvae forming serpentine frass and silk tubes, and one western species, *C. marmoreana* (Heinrich), for which hosts and larval habits are unknown. The following six new species indicate that morphological diversity in this genus is greatest in the southwestern United States and Mexico.

### METHODS AND MATERIAL

A stereomicroscope with an ocular micrometer was used to examine and measure specimens. The forewing length was measured from the outer edge of the tegula at wing base to the outermost edge of the fringe scales at apex. Setae and cornuti were counted by examining their sockets with a compound microscope. The “Methuen Handbook of Colour” (Konerup and Wanscher, 1983) was used as a standard for describing colors of imagos as observed under an incandescent light source.

Descriptions of the forewing are based on a comparative study of pattern elements in more than 600 tortricid species representing all tribes as defined by Horak and Brown (1991). The terminology for pattern elements is based largely on Nijhout



Fig. 1. *Catastega nebula*, n. sp., holotype, forewing with pairs of costal strigulae labeled 1–10.

(1978), as modified and discussed by Brown and Powell (1991). The term umbra is used for narrow, transverse lines of scales in fascial or interfascial areas that contrast with the paler ground color; the term spot is used for contrasting pigmentation that is confined to a restricted portion of a fascia (e.g., pretornal spot) or an interfascial area (e.g., white interfascial spot between subbasal and median fasciae in Figs. 2 and 3). The term patch is used to describe a color field that differs from the ground color and that covers at least one fascia and one interfascial area. The term stria is used for narrow, transverse lines of gray (silver when viewed at an appropriate angle to light) scales that originate at the costal strigulae and extend towards the inner or outer margin. Costal strigulae, which mark the margins of fasciae and usually occur in pairs, are numbered 1 to 10 from base to apex (Fig. 1).

Unidentified Olethreutinae and specimens identified as *Epinotia*, with which *Catastega* has been confused, have been borrowed from 27 institutions and several private collections. Specimens of the following new species of *Catastega* were borrowed from or are deposited in the collections of the following: André Blanchard (AB, deposited in USNM), American Museum of Natural History, New York (AMNH), Cornell University Insect Collection (CUIC), Edward C. Knudson, Houston, TX (ECK), Richard L. Brown, Mississippi State, MS (RLB), University of California, Berkeley (UCB), University of Connecticut, Storrs (UCONN), U.S. National Museum of Natural History (USNM).

#### KEY TO THE SPECIES OF *CATASTEGA*

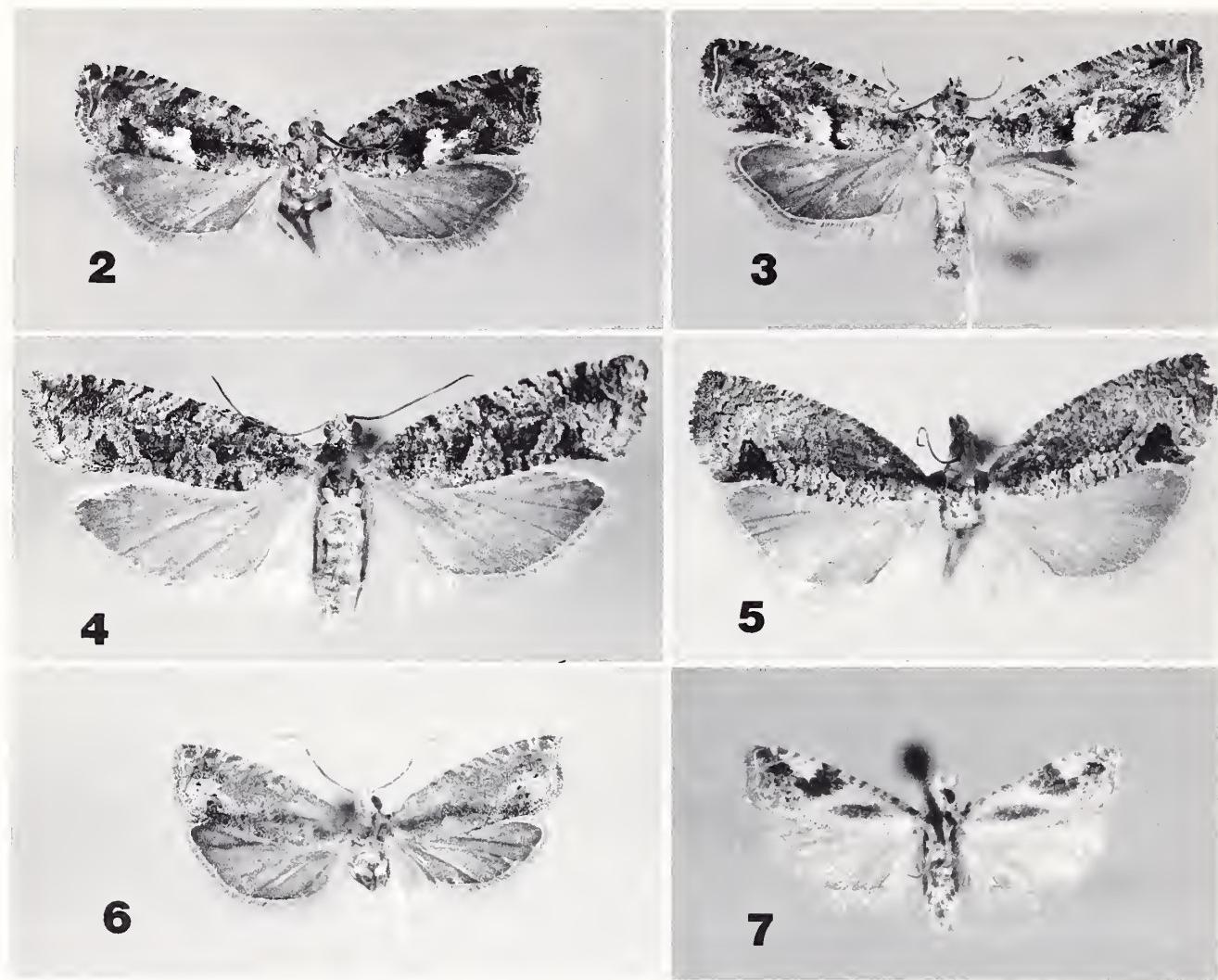
1. Forewing with pale yellow ground color, subbasal fascia forming longitudinally elongate spot between middle of discal cell and CuP . . . . . *plicata*, n. sp.

- Forewing ground color grayish brown, brownish gray, or brownish red, subbasal fascia extending to costa or inner margin or not forming contrasting spot ..... 2
- 2. Forewing with brownish red ground color, without contrasting fasciae ..... *adobe*, n. sp.
- Forewing ground color not brownish red, with or without contrasting fasciae ..... 3
- 3. Forewing with termen slanted towards tornus, apex acute, interfascial areas distinctly strigate ..... *strigatella*, n. sp.
- Forewing with termen not slanted towards tornus, apex not acute, interfascial areas not distinctly strigate ..... 4
- 4. Forewing with brown, triangular, pretornal spot, without other contrasting fasciae .....
- ..... *triangulana*, n. sp.
- Forewing with or without brown, pretornal spot, with other contrasting fasciae ..... 5
- 5. Forewing with subbasal fascia and pretornal spot not distinct on inner margin, pale inner marginal half and dark costal half separated by sinuate border .. *timidella* Clemens
- Forewing with subbasal fascia and pretornal spot distinct on inner margin, inner marginal half not contrastingly paler than costal half nor separated by sinuate border ..... 6
- 6. Ocellar area of forewing with well separated silver striae enclosing large group of peppered scales; male costal fold present or absent; occurring west of a line between San Antonio, Texas, and Winnipeg, Manitoba ..... 7
- Ocellar area of forewing with approximate silver striae not enclosing large group of peppered scales, male costal fold absent; occurring east of a line between San Antonio, Texas, and Winnipeg, Manitoba ..... *aceriella* Clemens
- 7. Forewing with pretornal spot contrastingly darker than median fascia on costa, without white interfascial spot on inner margin, male costal fold present; female sterigma surrounded by sternum VII ..... *marmoreana* (Heinrich)
- Forewing with pretornal spot usually not darker than median fascia on costa, with or without white interfascial spot, male costal fold absent; female sterigma posterior to sternum VII ..... 8
- 8. Silver stria between pretornal spot and postmedian fascia with irregular distal margin, ocellar area with many white scales; male cucullus rounded ventrally; occurring in Arizona ..... *nebula*, n. sp.
- Silver stria between pretornal spot and postmedian fascia with even distal margin, ocellar area with few white scales; male cucullus angled ventrally; occurring in Texas .....
- ..... *spectra*, n. sp.

**Catastega spectra, new species**

Figs. 2, 8, 9, 15

*Description.* Head: vertex grayish brown anteriorly, light grayish brown posteriorly, posterior scales with apices white to orange gray; labial palpus light grayish brown, second segment with orange-white or orange-gray scales on ventral base and with concolorous band on dorsal surface near two-thirds length, band becoming diffuse laterally and extending towards apex of ventral scale tuft. Thorax: mesonotum light grayish brown with white-tipped scales, with dark grayish-brown, transverse band at middle and concolorous semicircular band on posterior lobe, semicircular band approximate to transverse band at midline, bands diffuse and less distinct in some specimens; tegula usually dark grayish brown basally, light grayish brown or light grayish orange intermixed with yellowish white apically, most scales with white tips, some specimens with small, brownish orange or grayish orange spot surrounded by dark grayish brown at base. Forewing (Fig. 2): length 7.0–7.7 mm in males, 6.7–7.7 mm in females; male costal fold absent; termen concave, with indistinct white strigula



Figs. 2-7. *Catastega* n. spp. imagoes, all photographed at same magnification. 2. *C. spectra*, male Mt. Locke, Texas. 3. *C. nebula*, male, Chiricahua Mts., Arizona. 4. *C. strigatella*, female, Guadalupe Mts., Texas. 5. *C. triangulana*, female, Santa Rita Mts., Arizona. 6. *C. adobe*, holotype, male, Chiricahua Mts., Arizona. 7. *C. plicata*, male, Santa Rita Mts., Arizona.

between  $R_5$  and  $M_1$ ; costa with eight pairs of white to yellowish white strigulae apparent, pairs 1-4, 9, and 10 separate, 5 approximate to 6 and 7 approximate to 8 with each of two pairs appearing as single pair, strigulae separated by dark grayish-brown fasciae and umbrae; ground color light grayish brown, most scales with white to yellowish white tips, some specimens with large, white (as in Fig. 2) or small, brownish orange interfascial spot on inner margin; fasciae incomplete, dark grayish brown, broken transversely to form umbrae or longitudinally to form spots; basal fascia represented by narrow umbrae and isolated, small groups of scales; subbasal fascia represented by narrow, isolated umbra on costa and large, subquadrate spot on inner margin, outer margin of spot slanted toward wing apex, some specimens with subbasal spot confluent with median fascia at midwing; median fascia narrow on costa between strigulae 4 and 5, becoming broader at midwing, broken by ground color or white and one or two, small, transverse, gray (silver) bars at  $CuA_2$  to form triangular pretornal spot, spot enclosing 2-3, small, transverse, gray (silver) bars near inner margin and 2-3, small, longitudinal dark brown bars near midwing, median fascia with scales more peppered with yellow white apices than scales in subbasal

fascia; postmedian fascia narrow on costa between strigulae 6 and 7–8 and extending toward termen, angled towards tornus and widened near  $R_5$  to form spot enclosing 2–3 small groups of dark-brown scales, fascia enclosing small, gray (silver) bar at tornus, scales between  $R_5$  and tornus more peppered with white apices than scales in median fascia, postmedian fascia bordered distally and proximally by wide, gray (silver) striae, proximal stria with distal margin even and not broken by scales of postmedian fascia; grayish brown scales in costal and terminal areas apical to strigulae 7–8 with orange color when viewed at angle to light; outer margin with bases of attenuate fringe scales white to orange white, forming terminal line from apex to midway between  $CuA_1$  and  $CuA_2$ ; fringe between apex and tornus with proximal scales dark grayish brown with white apices, distal scales light brownish gray, without white apices except at terminal strigula between  $R_5$  and  $M_1$ . Underside brown except for yellowish white costal strigulae 3–10, scales in terminal area between strigulae 9 and tornus with white tips. Hindwing: upperside uniformly light brown; underside light grayish brown with distinct ripples of yellowish white on costa and indistinct ripples on terminal area between  $M_1$  and  $CuA_1$ .

Male genitalia (Figs. 8, 9): tegumen moderately broad, densely setose posterolaterally, moderately setose dorsomedially; uncus with forks well separated at their bases, forks sharply bent posteriorly at near midlength, each fork densely setose dorsally from near midlength to below its base; socius subquadrate, dorsoapically rounded, ventroapically fusing with base of gnathos, densely setose laterally from dorsal margin to base of gnathos except for smooth, rimlike, apical margin, vertical length of setose area at apical margin  $0.50\text{--}0.53 \times$  the length of straight line distance from ventral base of tegumen to base of uncus forks; aedeagus with 18 cornuti; anellus cuplike, not closely surrounding aedeagus, dorsal side elongate, length subequal to that of aedeagus, medially cleft; valva with elongate cluster of spiniform setae on sacculus, costa not indented distal to costal hook, dorsal and ventral margins of valva subparallel at middle third, cucullus elongate, apical margin forming obtuse angle with ventral margin of valva (two preparations examined).

Female genitalia (Fig. 15): sternum VII with scales sparse laterally, dense postero-medially, with a few rugae posterolaterally; tergum VIII with sparse setae and scales scattered on lateral extensions, each extension lateral to bases of apophyses with less than 20 scales and setae, dorsum with sparse setae; papillae anales with lateral and medial margins of each ventral surface subparallel, not expanded posteriorly, densely setose, some lateral setae with well-developed, papillose bases, rugae absent; sterigma conical, lamella antevaginalis well developed, without rugae, lamella postvaginalis reduced to narrow rim, posterolateral angles acute, setae absent; ductus bursae encircled by colliculum, moderately long on one side, sinewy, ductus expanded anteriorly before corpus bursae; signa subequal in size or with one signum smaller (three preparations examined).

*Holotype.* Male, labeled "McDonald Obser., Mt. Locke, Tex., 19-VII-1971, A. Blanchard." The type locality at McDonald Observatory is located 6,828 ft above sea level in Jeff Davis Co. The holotype is in excellent condition and is deposited in the U.S. National Museum of Natural History. Of the variation within the species, the holotype has an interfascial area on the inner margin between the subbasal and median fasciae that is light brownish gray, enclosing a small brownish orange spot (as in Fig. 1).

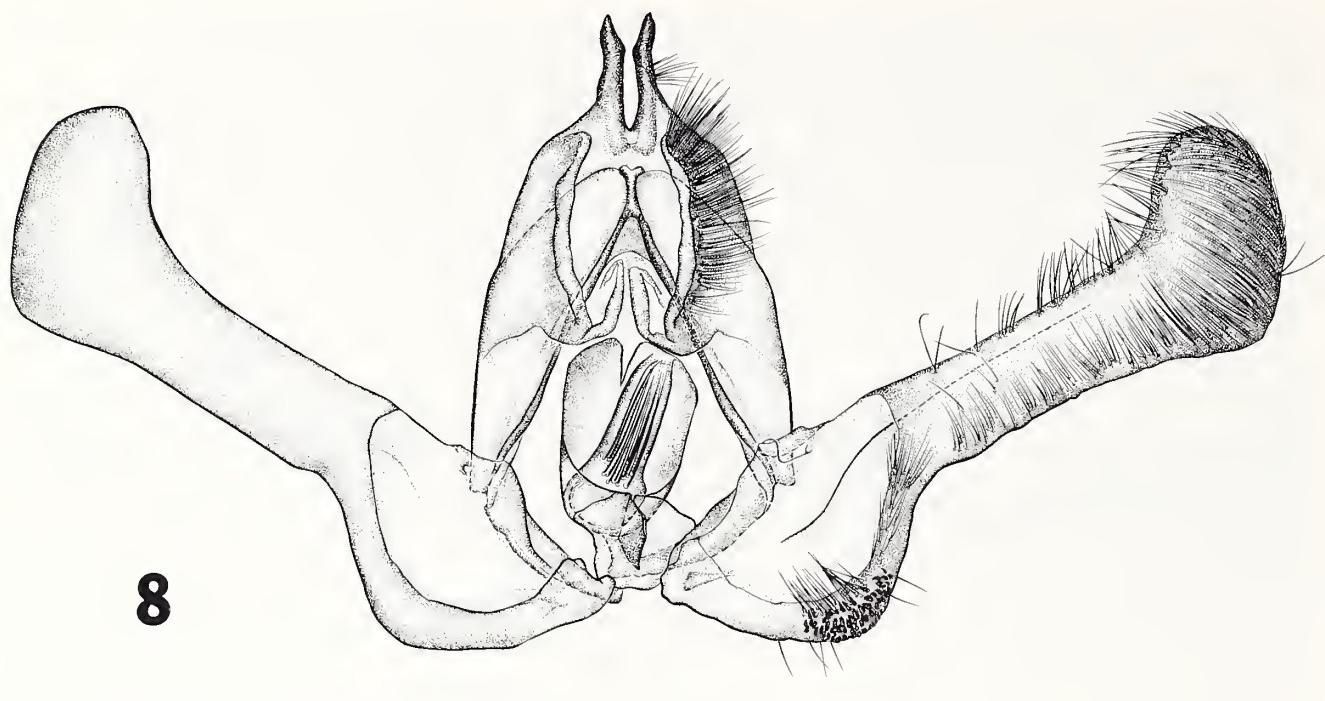


Fig. 8. *Catastega spectra*, n. sp., male genitalia, USNM slide 16026, Mt. Locke, Texas. Scale = 1 mm.

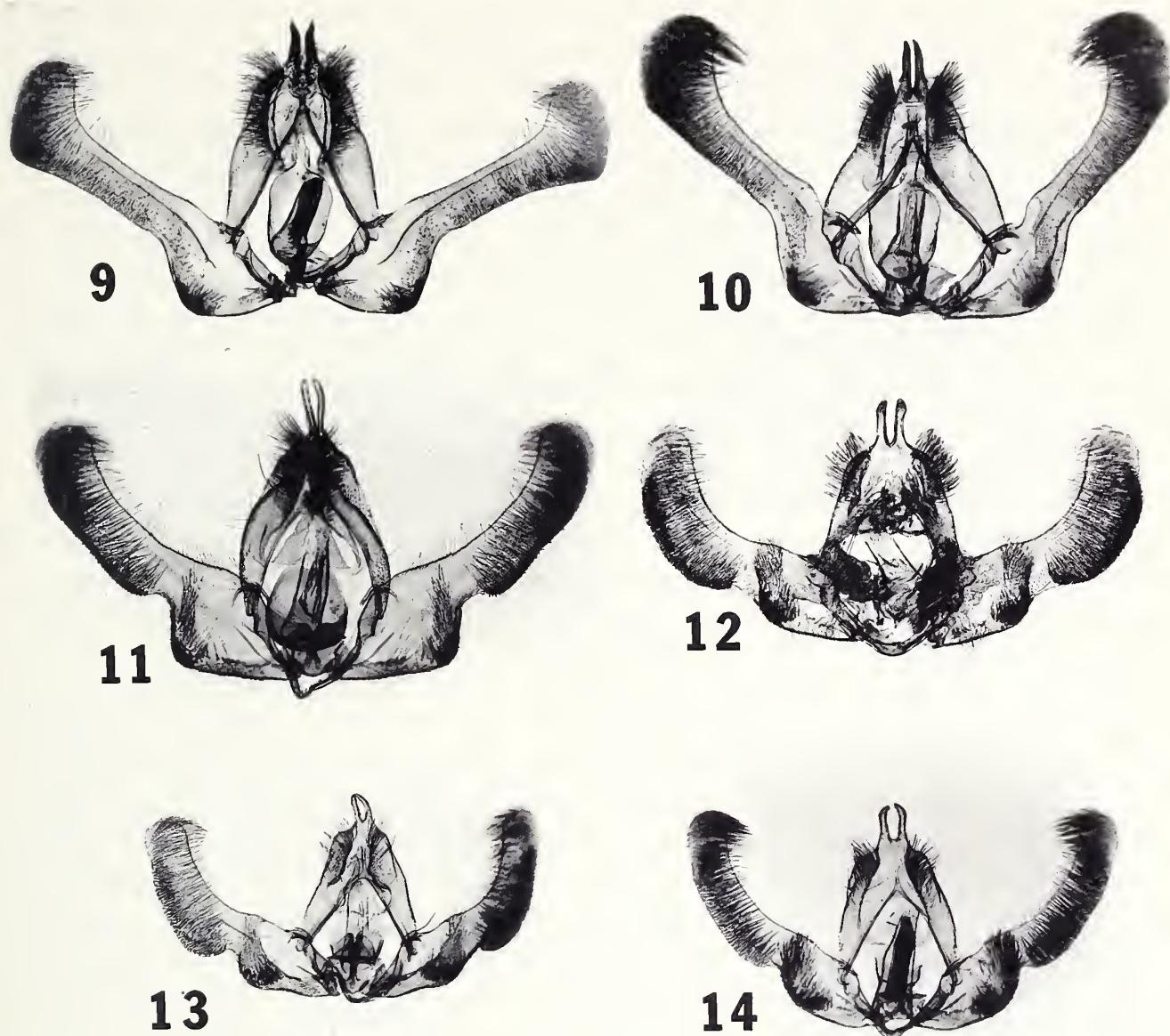
*Paratypes.* United States. Texas: same data as holotype, 11 males, genitalia slides USNM 16026, 17771, 4 females, genitalia slides USNM 17649, 17753, 17754 (RLB, USNM).

*Diagnosis.* Among previously described *Catastega*, *C. spectra* is most similar in genitalia to *C. aceriella* and *C. timidella*. The new species is superficially distinct by the light brown hindwing, the more contrasting subbasal and median fasciae, and the contrasting lightly pigmented area between these two fasciae on the inner margin. Distinctive characters of male genitalia include an uncus with forks that are well separated at their bases and that are bent posteriorly, an anellus with the dorsal plate subequal in length with the aedeagus, and a valva with the medial third having subparallel dorsal and ventral sides and with the apical margin of the cucullus forming an obtuse angle with the ventral margin. The female genitalia of the three species are similar in form, but the new species differs in having a wider tergum VIII, narrower papillae anales, a longer, smooth lamella antevaginalis that ventrally covers the ostium, and narrower signa. *Catastega spectra* is very similar in forewing pattern and genitalia to a new species from Arizona, which is differentiated in the following description.

#### *Catastega nebula*, new species

Figs. 1, 3, 10, 16

*Description.* Head and thorax: as in *C. spectra*. Forewing (Figs. 1, 3): as in *C. spectra* except length 7.7–8.5 mm in males, 7.8–8.6 mm in females; costa with 9 pairs of strigulae apparent, with pairs 5 and 6 separate and distinct; median fascia more narrow and less defined between costa and midwing; postmedian fascia between midwing and tornus with white scales intermixed with brown and dark grayish brown



Figs. 9–14. *Catastega* n. spp., male genitalia, all photographed at same magnification. 9. *C. spectra*, USNM slide 16026. 10. *C. nebula*, USNM slide 17738. 11. *C. strigatella*, AB slide 3765 (in USNM). 12. *C. triangulana*, holotype, USNM slide 28866. 13. *C. adobe*, USNM slide 17778. 14. *C. plicata*, holotype, USNM slide 17769.

scales with white tips, proximal margin of fascia and distal margin of gray stria irregular, with gray stria often broken by white or white-tipped scales of fascia. Hindwing: underside light grayish brown with indistinct ripples of yellowish white on costa and without ripples on terminal area between  $M_1$  and  $CuA_1$ .

Male genitalia (Fig. 10): as in *C. spectra* except uncus with forks curved posteriorly, not strongly bent, dorsum of each fork setose on basal one-fourth; socius with apical margin of lateral surface densely setose, vertical length of setose area at apical margin of socius  $0.37\text{--}0.40 \times$  the length of straight line distance from ventral base of tegumen to base of uncus forks, medial surface with smooth rim on apical margin; aedeagus with 22–30 cornuti; valva with base of costa deeply indented distal to costal hook, cucullus rounded ventrally (five preparations examined).

Female genitalia (Fig. 16): as in *C. spectra* except sternum VII of some specimens

with rugae lateral to midline from anterior to posterior margins; tergum VIII with setae and scales concentrated on posterior margins of lateral extensions, each extension lateral to bases of apophyses with more than 30 scales and setae; papillae anales with each ventral face narrow anteriorly, expanding posteriorly, lateral margin rugose; lamella antevaginalis with longitudinal rugae (three preparations examined).

*Holotype.* Male, labeled "Rustler Park 8500', Chiricahua Mts., Ariz. VII-14-72, at light, J. Powell. male genitalia slide 310 R.L. Brown." The type locality is in Cochise Co., Arizona. The holotype is deposited at University of California, Berkeley.

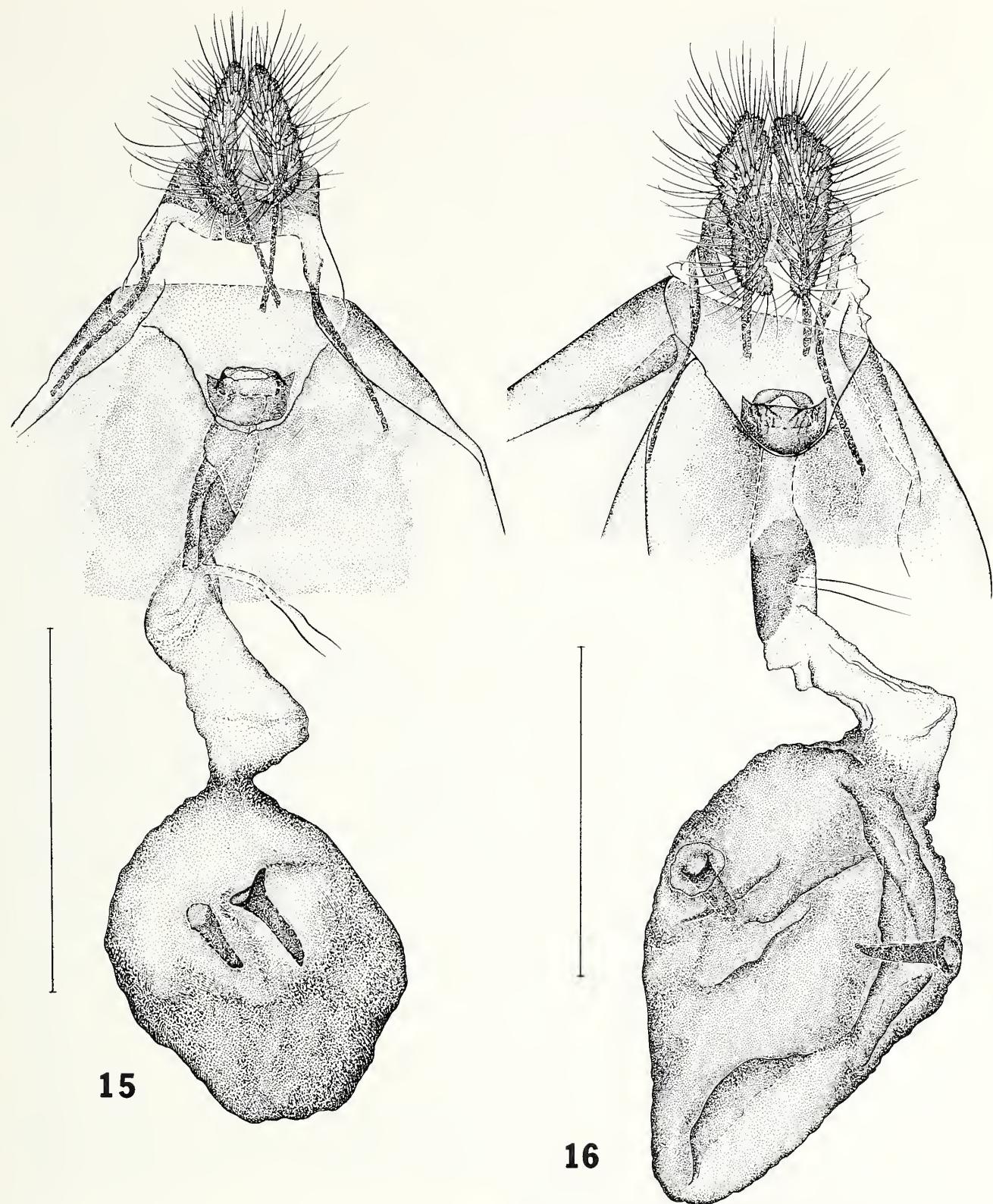
*Paratypes. United States. Arizona:* Cochise Co.: same data as holotype, 7 males, genitalia slides JAP 3629, RLB 1768, 3 females, genitalia slide RLB 311; same data except 3 July 1972, 1 male, RLB photo 159 on file, 12 July 1972, 2 females, genitalia slide RLB 621; Cave Creek, 1 mi SW Portal, 24–29 July 1972, J. Powell, 1 male, genitalia slide JAP 3626; Huachuca Mts., Carr Canyon, 5,300 ft, 29 July 1986, D. L. Wagner, 1 female. Santa Cruz Co.: Santa Rita Mts., Madera Canyon, 5,100 ft, Bog Springs Campground, July 10–26 1964, D. R. Davis, 2 males, genitalia slides USNM 17738, 28867; Madera Canyon, 4,880 ft, 25 Jul. 1959, R. W. Hodges, 1 female, genitalia slide RLB 382, 13 Aug. 1959, 1 female, genitalia slide RLB 383 (deposited in CU, RLB, UCB, UCONN, USNM).

*Diagnosis.* Differences in wing pattern between *C. spectra* and *C. nebula* are subtle but are consistent among specimens examined. The separation of costal strigulae 5 and 6 and the irregular distal margin of the gray (silver) stria between the pretornal spot and postmedian fascia are the most distinctive forewing characters for distinguishing *C. nebula*. The postmedian fascia in *C. nebula* has many white scales in the area of the ocellus, and these are lacking in *C. spectra*; however, the degree of pigmentation of the fasciae is a variable character in some species of *Catastega*. The setation of the apical margin of the lateral surface of the socius, in contrast to a smooth margin in related species, is a result of the socius being apically inflected inwardly, such that the medial surface is also setose apically. In addition, the setose area of the socius is vertically shorter in *C. nebula* than in *C. spectra*, and this is independent of the difference in the size of body, as indicated by forewing lengths.

#### ***Catastega strigatella*, new species**

Figs. 4, 11, 17

*Description.* Head: vertex and labial palpus brownish gray, scales with white to light gray apices. Thorax: mesonotum brownish gray with two, transverse, dark brownish gray bands on posterior half, with area between bands and posterior end light gray to white; tegulae basally dark brownish gray, apically light brownish gray with increasing amount of white to light gray on apices of scales. Forewing (Fig. 4): length 8.2–9.3 mm in males, 8.3–9.7 mm in females; male costal fold present, length of fold 0.39–0.41 × forewing length; termen straight, slanted towards tornus to produce acute angle at apex, with light gray strigula between  $R_5$  and  $M_1$ ; costa with nine pairs of light gray strigulae apparent, pairs 1 and 2 separate, poorly expressed, 3 and 4 approximate, appearing as two pairs, 5 and 6 separate, 7 and 8 confluent, appearing as one pair, 9 and 10 separate; ground color light brownish gray, some specimens light gray on costal half of wing, apices of scales varying in amount of light gray; fasciae usually incomplete, dark grayish brown; basal fascia indistinct except for



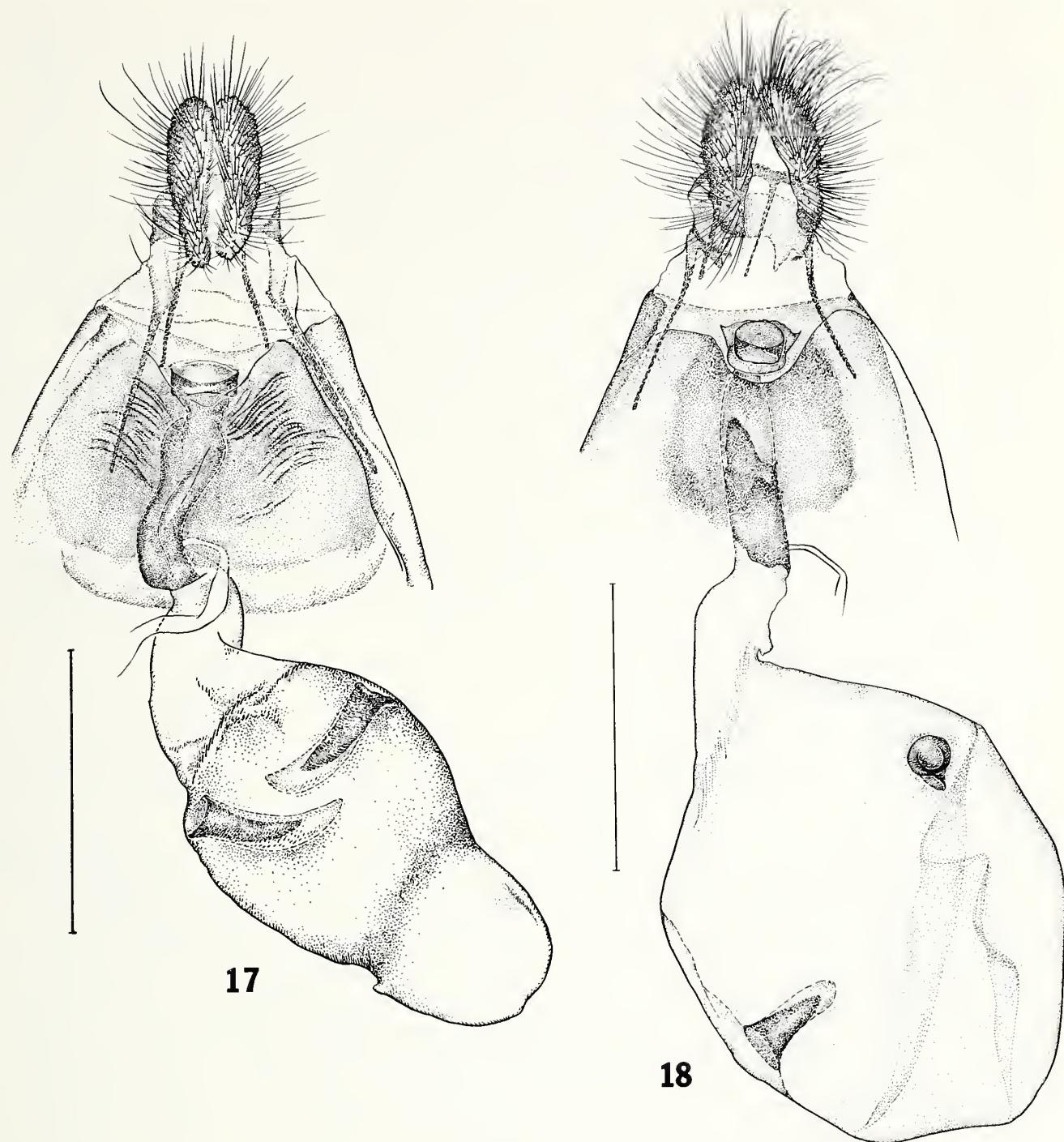
Figs. 15–16. *Catastega* n. spp., female genitalia. 15. *C. spectra*, USNM slide 17753. 16. *C. nebula*, RLB slide 621 (in UCB). Scale = 1 mm.

distal margin, extending as umbra from near costa to near inner margin; subbasal fascia complete from costa to inner margin in some specimens, outwardly angled near midwing, usually broken transversely at midwing or near CuP to form contrasting subquadrate spot on inner margin, proximal and distal margins of spot often dark grayish brown and enclosing brownish gray scales with gray apices, proximal

margin of spot extending as umbra from inner margin to CuP, distal margin extending as umbra from inner margin to CuP or midwing, margins of fascia usually distinct from costa to radius; median fascia broken into costal spot extending from costa to radius, medial spot extending from midwing to CuA<sub>2</sub>, and triangular pretornal spot extending from inner margin to CuA<sub>1</sub> when most expressed, proximal and distal margins and central areas of spots concolorous with those of subbasal inner marginal spot, costal spot usually indistinct, often with only margins expressed, medial spot wide at midwing, becoming narrow toward CuA<sub>2</sub>, spot crossed by oblique, dark, brownish gray line, usually with one or two umbrae between CuA<sub>2</sub> and inner margin; postmedial fascia represented by narrow umbra extending from costa to M<sub>3</sub>, often broken near R<sub>3</sub> and appearing connected with interfascial umbrae between strigulae 7 and 8 or with umbra of subterminal fascia between strigulae 8 and 9, ocellus absent, area between M<sub>3</sub> and CuA<sub>2</sub> (area of ocellus in related species) with two, short, approximate, gray striae appearing only slightly silver when viewed at angle to light; subterminal fascia reduced to umbra, broken near M<sub>3</sub>, appearing to originate from small spot between costal strigulae 9 and 10, extending to near CuA<sub>1</sub>, subparallel with postmedial umbra, area between these umbrae and between radius and midwing forming large spot (or patch from elements of postmedial and subterminal fasciae), concolorous with median and subbasal spots; terminal fascia represented at wing apex as small spot concolorous with other spots; outer margin without terminal line; fringe with each scale white to light gray at extreme apex, sharply contrasting with dark brownish gray at subapex, gradually becoming lighter brownish gray to gray from subapex toward base, proximal scales with irregular length and with white apices of scales not forming lines. Underside light grayish brown, costa with strigulae 4–10 distinct. Hindwing: upperside uniformly light grayish brown; underside light brownish gray, costal area with ripples of orange gray.

Male genitalia (Fig. 11): tegumen moderately broad, moderately setose postero-laterally, bare or with sparse setae dorsomedially; uncus with forks asetose, approximate and slender basally, gradually curved posteriorly, base of uncus with group of dense setae below each fork; socius strongly rounded dorsoapically, gently rounded ventrally to base of gnathos, lateral surface with apical third densely setose from dorsal margin to near base of gnathos, medial surface with smooth rim on apical margin; gnathos with base prolonged, arising from ventral one-third of vinculum; aedeagus with more than 31 cornuti; anellus cuplike, not closely surrounding aedeagus, dorsal side elongate, length about two-thirds that of aedeagus, dorsomedial margin concave; caulis short; valvae with small, elongate cluster of spiniform setae on ventroapical margin of sacculus, neck between cucullus and sacculus moderately constricted (four preparations examined).

Female genitalia (Fig. 17): sternum VII moderately setose laterally and anteriorly, densely setose posteromedially, rugose laterally; tergum VIII with apices of lateral extensions moderately scaled (20–25 each side) and sparsely setose (3–5 each side), dorsum sparsely setose; papillae anales with lateral margins evenly rounded, ventral face slightly broadest at one-third distance from posterior end, densely setose, lateral setae with moderately large, papillose bases, rugae absent; sterigma reduced, lamella antevaginalis forming a smooth, narrow rim around ostium, subequal in length with and superimposed on sclerotized posteroventral margin of ostium, lamella postvaginalis absent or reduced to very narrow portion of posterodorsal sclerotized margin



Figs. 17–18. *Catastega* n. spp., female genitalia. 17. *C. strigatella*, RLB slide 902 (in RLB). 18. *C. triangulana*, USNM slide 17688. Scale = 1 mm.

of ostium, setae absent; ductus bursae encircled by long, sinewy colliculum; signa subequal in size (three preparations examined).

*Holotype.* Male, labeled "Brewster Co., Tex., Big Bend Nat. Park, Chisos Basin, 29-III-82, Leg. E.C. Knudson." The specimen is in excellent condition and is deposited in the U.S. National Museum of Natural History.

*Paratypes.* Mexico. Coahuila: 17 mi SE Saltillo, 6,800 ft, 23 Sept. 1976, J. A. Chemsak & J. Powell, 1 male, genitalia slide JAP 5013, 1 female. United States. New Mexico: Otero Co.: 2 mi NE Cloudcroft, 8,600 ft, 1 Jul. 1964, F., P., & M. Rindge, 1 male. Socorro Co.: 28 mi SW Magdalena, 8,500 ft, 21 Jul. 1964, F., P., & M.

Ridge, 1 female, 22 Jul. 1964, 3 females, genitalia slide RLB 903. *Texas*: Brewster Co.: same data as holotype, 3 males, genitalia slides RLB 1147, ECK 287, 6 females, genitalia slide RLB 1148; Big Bend Nat. Park, Green Gulch, 31 Mar. 1970, A.&M.E. Blanchard, 1 male, genitalia slide AB 3765, 1 female, genitalia slide RLB 902, 3 Apr. 1984, E. C. Knudson, 1 male, 5,400', 2-4 Apr. 1986, E. C. Knudson, 1 male. Culberson Co.: Guadalupe Mts., McKittrick Canyon, 5,000 ft, 23 May 1973, R. W. Hodges, 1 male, genitalia slide USNM 17654; Guadalupe Mts, Smith Canyon, 22 May 1973, A.&M.E. Blanchard, 1 female, RLB photo 51 on file; Guadalupe Mts. N.P., Frijole, 29-31 Mar. 1990, E. C. Knudson, 1 male, same data except Ship on the Desert, 1 male, 1 female. Jeff Davis Co.: Davis Mts. St. Pk., 5 Jun. 1986, E. C. Knudson, 1 female (deposited in AMNH, ECK, RLB, UCB, USNM).

*Diagnosis.* The strigate interfascial areas, fascial pattern, and the slanting termen of the forewing differentiate this species from other *Catastega*. This species also differs from others in having a dark longitudinal line crossing the medial spot of the median fascia and a subterminal umbra that is broken from its origin between strigulae 7 and 8 and is reconnected with the interfascial umbra originating from between strigulae 9 and 10. The male genitalia are unique in having a socius that is ventrally lengthened and tapered into the long base of the gnathos. The valva has a well-defined neck separating the cucullus from the sacculus, similar to *C. marmoreana* and the following three new species.

***Catastega triangulana*, new species**

Figs. 5, 12, 18

*Description.* Head: vertex and labial palpus light grayish brown, posterior scales of vertex with light gray apices. Thorax: mesonotum grayish brown to light brown, scales with light gray apices, light gray increasing posteriorly; tegulae light brown, some specimens with apices of posterior scales light gray. Forewing (Fig. 5): length 6.7-7.3 mm in males, 7.3-7.9 mm in females; male costal fold present, length of fold 0.38-0.41 × forewing length; termen straight, not slanted toward tornus, without distinct strigulae, some specimens with lighter fringe scales between apex and  $R_5$ , between  $R_5$  and  $M_1$ , and on each side of  $CuA_2$ ; costa with five pairs of light brownish gray strigulae apparent, strigulae less distinct in some specimens, pairs 5 and 6 separate, 7 and 8 confluent, appearing as one pair, 9 and 10 separate; ground color brownish gray, specimens varying in number of scales with light-gray apices; fasciae as in *C. strigatella* except only pretornal triangle on inner margin well expressed, brown with dark brown margins or uniformly dark brown; costal two thirds from wing base to outer margin of median fascia forming indistinct grayish brown patch, slightly darker than ground color; subbasal fascia expressed as two dark brown umbrae from  $CuP$  to inner margin; postmedian fascia represented by dark brown umbra extending from between costal strigulae 6 and 7 to tornus, dentate and broken in area of ocellus between two, short gray (silver) striae; subterminal fascia extending from between costal strigulae 8 and 9 to near  $CuA_1$ , subparallel with postmedian umbra, some specimens with subterminal and postmedian umbrae connected by short, longitudinal line near  $M_2$ ; terminal fascia indistinct. Underside grayish brown, costa with strigulae 5-10 distinct in some specimens. Hindwing: upperside uniformly

light grayish brown; underside light brownish gray, some specimens with costa orange gray, without ripples.

Male genitalia (Fig. 12): as in *C. strigatella* except uncus with forks less slender basally, setose to midlength; socius strongly rounded dorsoapically and ventroapically, apical margin concave; gnathos arising from ventral base of socius at middle third of tegumen; aedeagus with approximately 20 cornuti; valva with sacculus gently rounded apically, neck and cucullus broad (two preparations examined).

Female genitalia (Fig. 18): as in *C. strigatella* except sternum with rugae very fine, becoming stronger anteriorly; tergum VIII with lateral extensions reduced to narrow bars, densely scaled and sparsely setose, dorsum without setae, anterior margin with two triangular extensions; sterigma less reduced, lamella antevaginalis forming a smooth, moderately broad rim around ostium, longer than sclerotized posteroventral margin of ostium, lamella postvaginalis moderately long, posterolateral angles with or without single seta; colliculum of ductus bursae long, not sinewy (two preparations examined).

*Holotype.* Male, labeled "4 mi ESE Pine, Gila Co. Ariz. 5400 ft, 1 September 1961, Ronald W. Hodges. Genitalia slide by R.L. Brown, USNM 28866." The holotype, which is missing the left mesothoracic leg, is deposited in the U.S. National Museum of Natural History.

*Paratypes. United States. Arizona:* Cochise Co.: Huachuca Mtns., Ash Canyon, 27–31 Jul. 1986, D. L. Wagner, 1 male; 2 mi SW Portal, 2–5 Aug. 1974, J. Powell, 1 male, genitalia slide RLB 1324. Gila Co.: same data as holotype, 1 female, genitalia slide USNM 17688. Pima Co.: Santa Rita Mtns., Madera Canyon, 4,400 ft, 10 Oct. 1959, R. W. Hodges, 1 female, genitalia slide RLB 297. Santa Cruz Co.: Santa Rita Mtns., Madera Canyon, 4,880 ft, 30 Jul. 1959, R. W. Hodges, 1 female, 5,600 ft, 17 Oct. 1959, 1 female (deposited in CU, RLB, UCB, UCONN, USNM).

*Other material examined.* The following specimens are tentatively identified as *C. triangulana* because of their similar forewing pattern and male genitalia: *Mexico. Durango:* 28 mi E El Salto, 8,000 ft, 22 Jul. 1964, [beating] *Arctostaphylos* sp., J. Powell, 3 males, same data except J. A. Chemsak & J. Powell, black & white lights, 8 males, genitalia slides JAP 1787, RLB 1423; 30 mi W Durango, 8,500 ft, 31 Jul. 1964, J. Powell, 2 males, 8,400 ft, 3–7 Aug. 1972, D. Veirs, J. Powell, C. D. MacNeill, 2 males, 1 female, 3–8 Aug. 1972, J. Powell & D. Viers, 1 male, 8,400 ft, Tepalcates, 4–8 Aug. 1972, 1 male, genitalia slide RLB 1334; 9 mi E La Ciudad, 9,000 ft, 23 Jul. 1964, J. Powell, 1 male. *Oaxaca:* 7 mi SE Nochixtlan, 7,000 ft, 7 Oct. 1975, J. Powell & J. Chemsak, 1 male.

These specimens (deposited in UCB) are not included in the type series nor in the description because they represent either a wide range of variation in *C. triangulana* or a distinct species. Unfortunately, both series are small, and the series from Mexico does not include females. The specimens from Mexico are larger, having a male forewing length of 7.8–9.2 mm, and the forewings appear slightly darker than specimens from Arizona. The forewing pattern of specimens from Mexico differs in having a more sinuate line of separation between the costal patch, extending from wing base to median fascia, and the lighter inner margin. This pattern difference, which falls within the range of variation of some *Catastega* species, is a result of the subbasal and median fasciae extending closer to the inner margin in specimens from Mexico than in those from Arizona. Male genitalia of specimens from Mexico, based on

examination of three slide preparations, differ in having a slightly more narrow, elongate, and apically constricted cucullus than those from Arizona; however, these may be allometric differences.

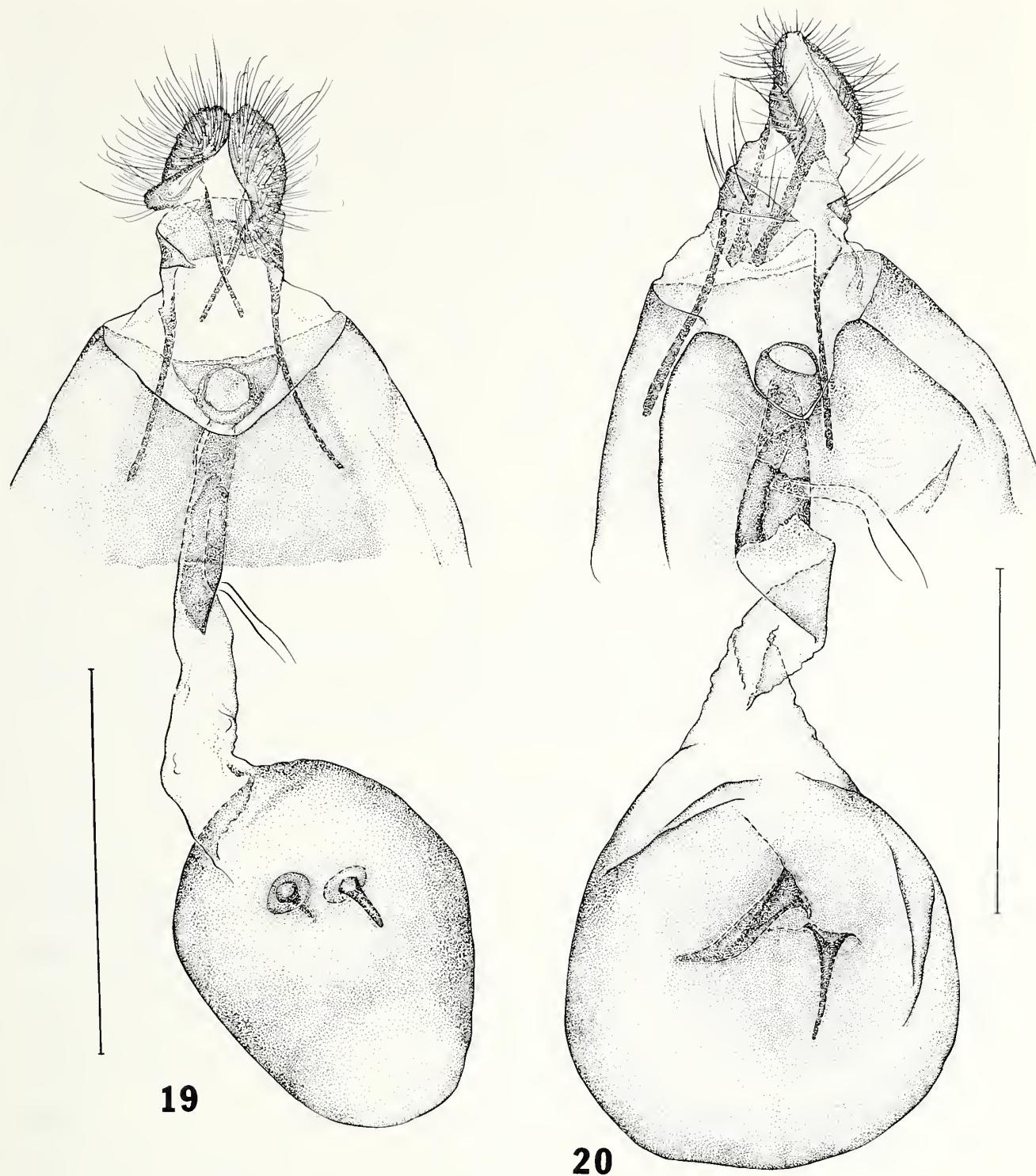
*Diagnosis.* This species and the following new species, *C. adobe*, both have the triangular pretornal spot as the most contrasting fascial element of the forewing pattern, which is unique among North American *Catastega*. The color and pattern of *C. triangulana*, however, is most similar to that of the *C. strigatella*. *Catastega triangulana* differs in its lack of expression of strigulae and fasciae and in having a suffusion of pigment in the interfascial areas between the basal, subbasal, and median fasciae; both subbasal and median fasciae are broken near the same vein in both species but are more expressed on the inner margin in *C. strigatella*. The male and female genitalia of *C. triangulana* are most similar to those of *C. adobe*; males of the two species differ slightly in shape of the valvae, and females differ in development of the sterigma, being more reduced in the latter species.

***Catastega adobe*, new species**

Figs. 6, 13, 19

*Description.* Head: vertex and frons yellowish white, becoming yellowish gray posterolaterally; labial palpus yellowish white with light brownish-gray band near apex of second segment. Thorax: mesonotum yellowish red anteriorly with tips of scales yellowish white, becoming brownish red posteriorly; tegulae brownish red. Forewing (Fig. 6): length 5.7–6.5 mm in males, 6.3–6.9 mm in females; male costal fold present, length of fold 0.33–0.35 × forewing length; termen slightly concave, strigulae absent; costa with five pairs of orange white strigulae apparent, strigulae 5, 6, 9, and 10 separate, strigulae 7 and 8 confluent, appearing as single pair; ground color brownish red; fasciae absent except for pretornal spot; outer two-thirds peppered by variable number of brown and grayish brown scales with white tips, some specimens more peppered with brown scales on median fold, pretornal area, area between ocellus and R<sub>4</sub>, and wing margins; pretornal spot brownish red suffused with variable number of peppered brown scales; ocellus weakly expressed, orange white, bordered by gray (silver) striae proximally and distally; outer margin with orange white terminal line formed from apices of distal row of disc scales and bases of attenuate fringe scales; fringe scales between apex and tornus with white apices, appearing peppered, proximal fringe brown, distal fringe grayish brown. Underside brown except for orange white costa and strigulae. Hindwing: light brown dorsally, light brown to grayish brown ventrally.

Male genitalia (Fig. 13): tegumen narrow ventrally, becoming moderately wide dorsally, sparsely setose laterally, bare dorsomedially; uncus moderately setose from base to midlength of forks; socius sub-triangular, expanded and bulbous dorsobasally, apical margin relatively straight from base of uncus to projecting ventral angle, irregularly serrate at high magnification, lateroapical half and medioapical third setose; gnathos arising from ventral bases of socii, well sclerotized basally; aedeagus with 10–18 cornuti; anellus not closely surrounding aedeagus, forming moderately shallow cup with long dorsal side, length less than half that of aedeagus; valva with sacculus and cucullus separated by neck without setae, sacculus with elongate, poorly



Figs. 19–20. *Catastega* n. spp., female genitalia. 19. *C. adobe*, USNM slide 17658. 20. *C. plicata*, USNM slide 17739. Scale = 1 mm.

defined cluster of spiniform setae on ventral margin, ventroapical corner strongly rounded, not overlapping base of neck (three preparations examined).

Female genitalia (Fig. 19): sternum VII with moderately dense scales throughout, more dense posteromedially, slightly rugose anteriorly; tergum VIII with lateral extensions reduced to narrow triangles, apices of lateral extensions setose and scaled, bare dorsally, anterior margin with two, short triangular projections; papillae anales densely setose, setae with small, papillose bases, rugae absent; sterigma with cone reduced, lamella antevaginalis narrow, lamella postvaginalis with 0–2 setae poster-

olaterally; colliculum of ductus bursae moderately sclerotized, long on one side, not encircling ductus; signa subequal in size and shape (three preparations examined).

*Holotype.* Male, labeled "Ariz. Cochise Co., Portal, 4 mi. W., 5300'; Chiricahua Mts., Aug. 3-6, 1964, D.R. Davis. Genitalia slide by R.L. Brown, USNM 17639. Photograph on file, 135 R.L. Brown." The holotype is in excellent condition and is deposited in the U.S. National Museum of Natural History.

*Paratypes.* United States. Arizona: Cochise Co.: same data as holotype, 3 males, genitalia slides USNM 17770, 17778, 1 female, genitalia slide USNM 17658. New Mexico: Lincoln Co.: Capitan Mts., near Nogal, 1 Aug. 1989, Wagner & Epstein, 1 male, 1 female. McKinley Co.: Ft. Wingate, Jul. 16-23 [year and collector unknown], 1 female, July 24-31, 1 female. Socorro Co.: 28 mi SW Magdalena, Bear Trap Camp, 6,500', July 6 1965, F., P. & M. Rindge, 1 female, July 7 1965, 1 male. Texas: Culberson Co.: Guadalupe Mts. N. P., McKittrick Canyon, 30-31 July 1989, Wagner, Epstein, & Knudson, 1 male, Dog Canyon, 6,400', 19-20 Aug. 1990, E. C. Knudson, 4 females; Sierra Diablo W.M.A., 27 Jun. 1981, E. C. Knudson, 1 male. Jeff Davis Co.: Mt. Locke, 27 May 1979, E.C. Knudson, 1 male (deposited in AMNH, ECK, RLB, UCONN, USNM).

*Diagnosis.* *Catastega adobe* differs from other *Catastega* and most other Olethreutinae in having brownish red forewings without contrasting fasciae (except for the triangular pretornal spot, which is derived from median fascia). The form of the socius in the male and the form of sterigma with reduced lamella antevaginalis and developed lamella postvaginalis in the female is diagnostic for this species.

### ***Catastega plicata*, new species**

Figs. 7, 14, 20

*Description.* Head: vertex pale yellow to yellowish white; labial palpus yellowish white, intermixed with grayish brown except ventrobasally and at two-thirds length. Thorax: mesonotum yellowish white to pale yellow anteriorly, becoming pale orange to grayish orange posteriorly; tegulae pale orange intermixed with grayish orange basally, becoming yellowish white apically. Forewing (Fig. 7): length 5.8-7.6 mm in males (5.8-6.8 mm in Arizona specimens; 6.0-7.6 mm in Mexico specimens), 5.8-8.3 mm in females (5.8-7.0 mm in Arizona specimens; 6.7-8.3 mm in Mexico specimens); male costal fold present, length of fold 0.56-0.62× forewing length; termen slightly concave, strigulae absent; costa in female with six pairs of yellowish white to orange white strigulae apparent, pairs 3, 4, 9 and 10 separate, pairs 5 and 6 and pairs 7 and 8 confluent, each confluent pair appearing as single pair, males as in females except with pairs 1-4 yellowish gray, with individual strigulae widely spaced on costal fold, strigulae 5-8 in both sexes with striae concolorous with ground color, indistinct except shiny when viewed at angle to light, strigulae 9 with stria gray (silver) from  $R_4$  to  $R_5$ , strigulae 10 with short gray (silver) stria extending to  $R_5$  or near termen; ground color pale yellow intermixed with variable amounts of yellowish white and pale orange, suffused with reddish orange to brownish orange on costal area between median fascia and apex and terminal area between apex and tornus; fasciae brown intermixed with variable amounts of dark brown and grayish orange; basal fascia absent; subbasal fascia forming longitudinally elongate spot between middle of discal cell and CuP, some specimens with fascia expressed between

costa and radius and/or with suffusion of grayish orange between CuP and inner margin; median fascia brown or brown intermixed with grayish orange, usually extending from costa to between CuA<sub>1</sub> and CuA<sub>2</sub>, rarely complete, some specimens with separate, sub-triangular pretornal spot, some specimens with dark brown, longitudinal streak on accessory cell, inner margin of fascia extending basally near costa beyond apices of strigulae 4; postmedian fascia expressed as large, rounded spot, dark brown intermixed with varying amounts of brown and/or grayish orange, separated from median fascia by ground color or suffusion of grayish orange; subterminal and terminal fascia not expressed; outer margin bordered by white to yellow white terminal line formed from bases of proximal attenuate fringe scales, pre-apical area of proximal fringe scales forming reddish orange line from apex to tornus, becoming more irregular towards latter, distal fringe scales uniformly grayish orange. Underside light grayish brown to grayish orange, costal area rippled by yellowish white to orange white strigulae. Hindwing: upperside yellowish gray to yellowish white, underside yellowish white.

Male genitalia (Fig. 14): tegumen narrow ventrally, becoming expanded at bases of socii, moderately setose laterally, sparsely setose dorsomedially; uncus setose from base to one-third length of forks, apices of forks curved medially; socius dorsobasally expanded, bulbous, apical margin gently rounded dorsoapically and tapered ventrally into bases of gnathos, irregularly serrate at high magnification, lateroapical half and medioapical third setose; gnathos arising from base of ventral socius; aedeagus with 28–32 cornuti; anellus appearing relatively reduced, sclerotized portion forming shallow cup, not closely surrounding aedeagus, dorsal and ventral sides of sclerotized portion subequal in length, dorsal side with lightly sclerotized extension reaching to two-thirds length of aedeagus; valva with sacculus and cucullus separated by neck without setae, sacculus with poorly defined cluster of spiniform setae on ventral margin, ventroapical corner strongly rounded, slightly overlapping base of neck (four preparations examined).

Female genitalia (Fig. 20): sternum VII with moderately dense scales throughout, more dense posteromedially, rugose medially, except for midline, from posterior to anterior margins; ovipositor (segment VIII and posteriorly) modified for insertion; tergum VIII with setae much longer than setae on papillae anales, sparse and random on well developed, triangular, lateral extensions, moderately dense in irregular row on dorsum, scales absent, anterior margin with long, rounded projection; papillae anales fused and attenuate posteriorly, setae moderately dense, bases not on papillae, setose surface wide laterally, narrow ventrally; posterior and anterior apophyses thick and wide with expanded bases; sterigma skewed, lamella antevaginalis well developed, smooth, lamella postvaginalis reduced to narrow rim, without posterolateral angles and setae; colliculum of ductus bursae moderately sclerotized, sinewy, long on one side; signa subequal in size and shape (four preparations examined).

*Holotype.* Female, labeled "Ariz. Santa Cruz Co., Madera Canyon 5100', Santa Rita Mts., July 10–26, 1964, D.R. Davis; Bog Spring Camp Ground; Genitalia Slide by R.L. Brown USNM 17769." The holotype is in excellent condition, except for missing the right prothoracic leg, and is deposited in the U.S. National Museum of Natural History.

*Paratypes.* Mexico. Durango: 3 mi E Revolcaderos, 11 Aug. 1972, J. Powell, 1 male; Durango, Arroyo los Mimbres, 2,200 m, 19 Aug. 1984, E. Welling, 1 male, 3

females; 10 mi W El Salto, 8,800 ft, 23 Jul. 1964, J. A. Chemsak & J. Powell, 1 female; 31 mi E El Salto, 18 Jul. 1964, J. A. Chemsak, 1 female, genitalia slide RLB 1413; 30 mi W Durango, 5 Aug. 1972, J. Powell, 1 male, 8,500 ft, 31 Jul. 1964, J. A. Chemsak & J. Powell, 1 male, 2 females, 8,400 ft, 3–8 Aug. 1972, J. Powell, D. Veirs, & C. D. MacNeill, 25 males, genitalia slide JAP 3734, 7 females, Tepalcates, 8,400 ft, 4–8 Jul. 1972, 6 males, genitalia slide RLB 1412, 1 female, same data without elevation, 11 Aug. 1986, Brown & Powell, 2 males, 2 females. *Sinaloa*: 8 mi W El Palmito 6,400 ft, 8–12 Aug. 1972, J. Powell, D. Veirs, & C. D. MacNeill, 1 male, 2 females, 6 Aug. 1986, J. Brown & J. Powell, 1 male. *United States. Arizona*: Cochise Co.: Huachuca Mts., Ash Canyon, 27–31 Jul. 1986, D. L. Wagner, 1 male, Carr Canyon, 5,300 ft, 29 Jul. 1986, D. L. Wagner or Wagner and Powell, 4 females. Pima Co.: Madera Canyon, Bog Springs, 30 Jul. 1973, J. Powell, 1 male. Santa Cruz Co.: same data as holotype, 1 male, 2 females, genitalia slide USNM 17739, same data plus "from flowers *Yucca schottii*," 1 male; Madera Canyon, 4,880 ft, 19 Jul. 1959, R. W. Hodges, 1 male, genitalia slide RLB 328, 25 Jul. 1959, 1 female, genitalia slide RLB 327, 5,600 ft, 1 Aug. 1959, 1 female, genitalia slide RLB 494, 4,880 ft, 2 Aug. 1959, 1 male, 4 Aug. 1959, 2 males, 1 female, 4,880 ft, 18 Aug. 1959, 1 male (deposited in CU, RLB, UCB, UCONN, USNM).

*Diagnosis.* The pale yellowish color combined with the forewing pattern of the subbasal and medial fasciae and postmedian spot in this species is unique among known North American Eucosmini. The length of the male costal fold in *C. plicata* and *C. marmoreana* is more than half the forewing length, whereas the costal fold is absent or much shorter in other *Catastega* species. Male genitalia differ from those of other known species by the combined forms of the socius and valva; female genitalia differ from other known species by the combined forms of the ovipositor and sterigma. The form of any one structure is similar to that in one or more other species of *Catastega*.

*Comments.* The female of *C. plicata* is considered to have a form of ovipositor for inserting eggs in crevices because of developed setae and loss of scales on the eighth tergum, reduced ventral faces of the papillae anales, and developed apophyses, which are characteristic of other species known to insert eggs in buds, bark crevices, and other constricted areas. In contrast to many species with inserting ovipositors, the ovipositor is not greatly lengthened and the moths fly during late summer, rather than early spring. The ovipositor of *C. plicata* is similar to that of an undescribed species of *Catastega* that occurs in southeastern United States; the latter species has a forewing pattern and male genitalia very similar to *C. timidella*. Although a single male has been collected from flowers of *Yucca*, the host remains unknown.

#### ACKNOWLEDGMENTS

I thank Dr. John G. Franclemont for his guidance during the period when I first began gleaning new species of *Catastega* from among unidentified Olethreutinae. I gratefully acknowledge Frederick H. Rindge (AMNH), L. L. Pechuman (CUIC), Edward C. Knudson, Jerry A. Powell (UCB), David L. Wagner (UCONN), Don R. Davis (USNM), and the late Andre Blanchard for the loan of specimens. Photographs of the imagoes, except Figure 1, were made by Howard Lyons; drawings were made by Amy Trabka, and plates were made by Joe MacGown.

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## PUPAL MORPHOLOGY AND THE SUBFAMILY CLASSIFICATION OF THE NOTODONTIDAE (LEPIDOPTERA: NOCTUOIDEA)

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*Abstract.*—Pupal morphology is surveyed among 46 species of Notodontidae representing all currently-recognized subfamilies, and 24 phylogenetically informative characters are identified. Comparison of a previous notodontid subfamily phylogeny based on larval and adult morphology with one constructed from pupal data shows close concordance. Although it was not possible to identify a synapomorphy for the Notodontidae from pupae, this life stage provides a long list of potential synapomorphies useful at the subfamily level.

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The immature stages of Lepidoptera provide crucial character information for studies in taxonomy and phylogeny. Unfortunately, our knowledge of pupal morphology is lagging behind the growing body of data on larvae. This can be attributed, at least in part, to a lack of available material. For example, in the North American Notodontidae, where larvae are known for the majority of species, preserved pupae are relatively uncommon in collections. Among tropical groups, the situation is dismal; in the Neotropical notodontid subfamily Dioptinae, larvae are known for about 4% of the fauna (Miller, 1992), and pupal material is available for less than 2%.

Use of pupal characters has a long history in Lepidoptera systematics. Among the earliest comparative studies are those of Jackson (1890), Poulton (1891), and Chapman (1892, 1893), all of whom stressed the potential taxonomic value of pupae. Early attempts at a phylogeny for the lepidopteran families (Packard, 1895; Chapman, 1896) relied heavily on pupal characters. Hinton's (1946) classification of insect pupae drew attention to the major subdivisions of the Lepidoptera. Pupae figure prominently in modern treatments as well. Minet (1991), in his recent phylogeny for the Ditrysia—by far the largest and most homogeneous part of the order (Nielsen, 1989)—identified several important pupal characters.

The preeminent worker on Lepidoptera pupae was Edna Mosher, whose papers form the basis for study even today. Her research uncovered characters useful in elucidating problematic family interrelationships that were intractable using adult or larval morphology. In addition to providing a general framework for pupal morphology and classification of the Lepidoptera (Mosher, 1916b), her work focused on the families Saturniidae (1914, 1916a) and Sphingidae (1918a). She also published the most comprehensive study available on pupae of the Notodontidae (Mosher, 1918b).

Pupae are taxonomically important in other families of Lepidoptera, an example being the Geometridae (Ridge, 1952; McGuffin, 1987; Bolte, 1990). Nakamura's

(1976) research on pupae of Japanese Lymantriidae treated 33 species in 16 genera. After identifying a set of useful characters, he subdivided the genera and provided a phylogeny. Common (1990), in his recent book on Australian moths, relied extensively on pupae for family-level diagnostic characters, providing pupal illustrations for representatives of all the Australian moth families.

There are distinct differences among lepidopteran groups in the form of the cocoon, in the mode of pupation, and in the method of escape by the adult from the cocoon and pupa (Hinton, 1946; Common, 1975). A well-known example from the Noctuidae is the unusual boat-shaped cocoon found in Sarrothripinae and Nolinae, which provides evidence of relationship between the two subfamilies (Forbes, 1954; Franclemont, 1960; Kitching, 1984).

Differences in cocoon structure and in the mode of pupation can also be found within the Notodontidae (Packard, 1895; Grünberg, 1912). For example, *Cerura* larvae excavate a shallow depression in a twig (usually on the foodplant) and construct an extremely dense cocoon formed from chewed wood particles and salivary secretions (Dyar, 1891; Chapman, 1892). When the adult moth emerges it produces a secretion from the head, possibly containing an enzyme (Kafatos and Williams, 1964), which dissolves the tough cocoon (Chapman, 1892; Hinton, 1946). Dolinskaya (1989) divided notodontids into two groups: those—such as *Cerura*, *Furcula*, *Glaphisia*, and *Closteria*—that pupate on the food plant, and those—such as *Phalera*, *Stauropus*, *Notodontia*, *Pheosia*, and *Spatialia*—that leave the host to pupate in the soil or litter. She further pointed out that in the first group of genera, all except *Closteria* exhibit reduction of the cremaster (see Character 20 below). Although characters relating to cocoon structure and pupation behavior will undoubtedly provide valuable information for future work on notodontid systematics, they were not used here simply because available data are scarce.

This paper is intended to compliment the pioneering works of Packard (1895), Mosher (1916b, 1918b), and Dolinskaya (1989) on notodontid pupae. Those authors demonstrated extensive variation in a variety of characters, and all used pupal traits in their subfamilial and generic diagnoses. However, their findings have not been examined in the context of a world-level classification. In a recent paper (Miller, 1991), I recognized nine subfamilies for the world Notodontidae. My cladistic hypothesis for those is shown in Figure 1. This paper is not a comprehensive treatment of pupae, but it provides an overview with two major aims: to identify potentially useful characters for notodontid phylogeny and classification, and more generally, to stimulate further interest in the morphology of this life stage. In particular, I stress the implications of pupal data for understanding subfamily relationships.

#### MATERIALS AND METHODS

Morphological terminology (see Fig. 2) follows Mosher (1916b) and Common (1990). Most of the pupae I studied had been preserved in alcohol. Intact pupae were examined in almost all cases, but where these were not available, exuviae were used. Line drawings were made using a camera-lucida attached to a Zeiss SV8 stereomicroscope. Scanning electron micrographs were taken with a Zeiss DSM950 microscope. Specimens for SEM were air-dried, mounted on stubs in silver paste, and then dried again overnight in an oven at 47°C before being coated with gold-palladium.

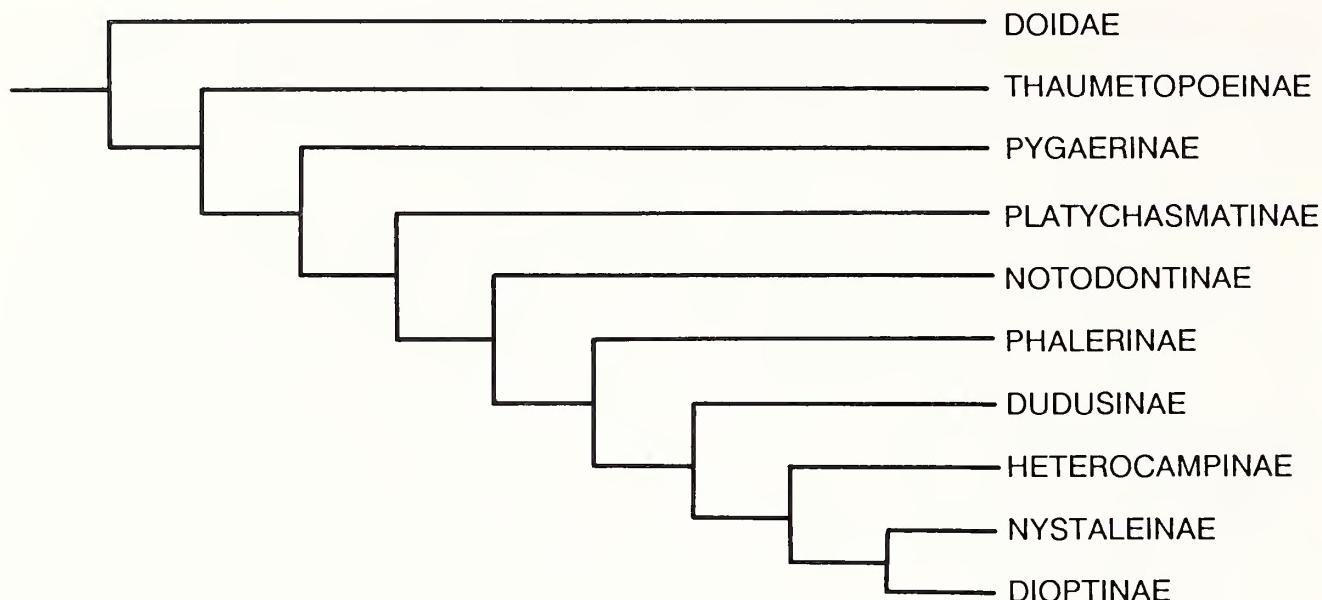


Fig. 1. Cladogram of subfamilies in the Notodontidae based on an analysis of 174 larval and adult characters (from Miller, 1991).

The list of species examined is shown in Table 1. Comprehensive study of outgroup taxa was beyond the scope of this paper. The Doidae—containing two relatively small genera, *Doa* Neumoegen and Dyar and *Leuculodes* Dyar (Franclemont, 1983; Donahue and Brown, 1987)—and Notodontidae are thought to be sister groups (Miller, 1991). I used pupae of *Doa ampla* (Grote) (Fig. 2) for outgroup comparison. The pupa of another doid, *D. dora* Neumoegen and Dyar, was figured by Brown (1990). I have generally relied on Mosher (1916b) in my assessment of pupal morphology among quadrifid Noctuoidea, but needless to say, this is a cursory approach; the group contains tremendous morphological variation, and Mosher's treatment is relatively brief.

I performed cladistic analyses using pupal characters scored for 16 notodontid species. These 16 taxa were chosen to represent the nine subfamilies recognized in Miller (1991). Twenty-four characters comprising 61 character states (Table 2) were identified. The resulting data matrix (Table 3) was then analyzed using the Hennig86 parsimony program of Farris (1988), with *Doa ampla* as an outgroup. Shortest trees were produced by implicit enumeration. The analysis provides a test of how pupae fit with my previous hypothesis of subfamily relationships based on adult and larval characters (see Fig. 1).

#### PUPAL MORPHOLOGY

Below is the list of characters for which I found useful variation. My treatment is preliminary; more characters certainly remain to be discovered, and it is impossible to fully assess morphological variation using such a small species sample. However, all the traits I discuss deserve consideration in future taxonomic research on the Notodontidae. Characters with numbers in parentheses were used in the cladistic analyses (see Table 2).

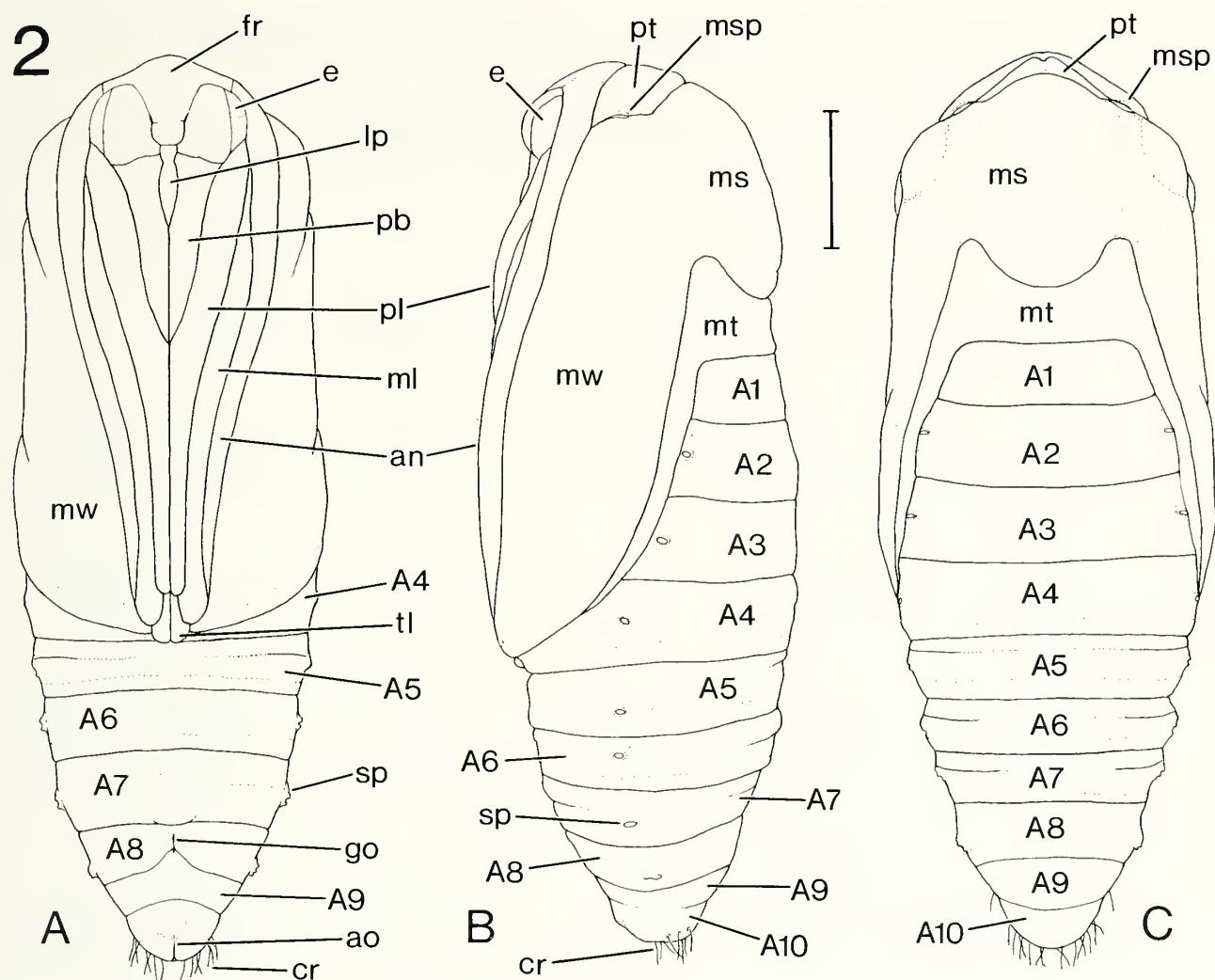


Fig. 2. Pupa of *Doa ampla* (Grote) (Doidae). A. Ventral view. B. Lateral view. C. Dorsal view. A = abdominal segment; an = antenna; ao = anal opening; cr = cremaster; e = eye; fr = front; go = genital opening; lp = labial palpi; ml = mesothoracic leg; ms = mesothorax; msp = mesothoracic spiracle; mt = metathorax; mw = mesothoracic wing; pb = proboscis; pl = prothoracic leg; pt = prothorax; sp = spiracle; tl = metathoracic leg. Scale line = 2 mm.

#### Head:

**Eyes.** (1) Mosher (1916b) recognized two parts of the eye in Lepidoptera pupae: one part she termed the "sculptured eye-piece," and the other the "glazed eye-piece." I found this division difficult to see, at least in notodontids, and the morphological distinction may be unnecessary for this group.

Mosher (1918b) identified an interesting character in her study of Maine notodontids. She noticed that in *Closteria* species, the proximo-lateral angles of the proboscis do not reach the eye-pieces (Fig. 4A). This is also illustrated by the pupae of *Doa ampla* (Fig. 2A) and *Thaumetopoea pinivora* (Fig. 3A). In most notodontids, the proximo-lateral angles of the proboscis reach the eye-pieces (Figs. 5A, 6A, 8A-12A). In *Cerura* and *Furcula* they do not (Fig. 7A), but in other Notodontinae they do (Fig. 8A). Thus, according to my survey only the Doidae, the Thaumetopoeinae, the Pygaerinae, as well as *Cerura* and *Furcula* of the Notodontinae, exhibit the first

Table 1. List of species for which pupae were examined arranged according to the classification of Miller (1991).

	Taxon	Locality	Collection
Doidae			
	<i>Doa ampla</i> (Grote)*	Arizona	CUIC
Notodontidae			
Thaumetopoeinae			
	<i>Thaumetopoea pinivora</i> (Treitschke)*	Germany	CUIC
Pygaerinae			
	<i>Closteria albosigma</i> Fitch*	New York	CUIC, NYSM
	<i>C. inclusa</i> Hübner	Illinois	INHS
Platychasmatinae			
	<i>Platychasma virgo</i> Butler*	Japan	SSC
Notodontinae			
Notodontini			
	<i>Notodontia similaria</i> Graef*	New York	NYSM
	<i>Pheosia portlandia</i> Hy. Edwards	Oregon	NYSM
	<i>Hyperaeschra georgica</i> Herrich-Schäffer	New York	CUIC
Dicranurini			
	<i>Cerura scitiscripta</i> Walker	Florida	AMNH
	<i>Furcula occidentalis</i> (Lintner)*	New York	AMNH
	<i>F. scolopendrina</i> (Boisduval)	New York	NYSM
	<i>F. modesta</i> (Hudson)	New York	NYSM
	<i>Gluphisia septentrionis</i> Walker*	New York	AMNH, CUIC
Phalerinae			
	<i>Datana robusta</i> Strecker	Texas	CUIC, USNM
	<i>D. integerrima</i> Grote and Robinson	New York	CUIC, NYSM
	<i>D. ministra</i> (Drury)*	New York	CUIC
	<i>D. drexelii</i> Hy. Edwards	New York	CUIC
	<i>D. contracta</i> Walker	New York	CUIC
	<i>D. angusii</i> Grote and Robinson	New York	CUIC
	<i>Phalera</i> sp.**	—	—
	<i>Ellida caniplaga</i> Walker	New York	CUIC
	<i>Nadata gibbosa</i> Smith	Illinois	INHS, NYSM
Dudusinae			
	<i>Crinodes besckei</i> Hübner*	Costa Rica	INHS
	<i>Goacampa variabilis</i> Schaus*	Costa Rica	INHS
Heterocampinae			
	<i>Heterocampa umbrata</i> Walker	Illinois	INHS
	<i>H. bilineata</i> Packard	Illinois	INHS
	<i>H. guttivitta</i> Walker*	New York	NYSM
	<i>Hyparpax aurora</i> (Smith)	New Jersey	AMNH, USNM
	<i>Lochmaeus manteo</i> Doubleday*	New York	NYSM
	<i>Misogada unicolor</i> Packard	New York	NYSM

Table 1. Continued.

Taxon	Locality	Collection
<i>Schizura ipomoeae</i> Doubleday	Connecticut	AMNH
<i>S. badia</i> (Packard)	New York	AMNH
<i>S. unicornis</i> (Smith)	New Jersey	AMNH
<i>S. concinna</i> (Smith)	Illinois	INHS
<i>Litodonta hydromeli</i> Harvey	Texas	SJW
<i>Spatalia argentina</i> (Schiffermüller)	Europe	CUIC
Nystaleinae		
<i>Didugua argentilinea</i> Druce*	Texas	USNM
<i>Symmerista albifrons</i> Smith*	Illinois	INHS
<i>S. leucitys</i> Franclemont	New York	NYSM
Dioptinae		
<i>Cyanotricha neocyria</i> Felder	Colombia	AMNH
<i>Josia ligula</i> Hübner*	Ecuador	SJW
<i>Phaeochlaena gyon</i> Fabricius	Brazil	BMNH
<i>Phryganidia californica</i> Packard	California	USNM
<i>Zunacetha annulata</i> Guérin*	Panama	AMNH
Incertae Sedis		
<i>Nerice bidentata</i> Walker	New York	NYSM
<i>Lophopteryx cuculla</i> Esper	Germany	CUIC
<i>Drymonia trimacula</i> Esper	Germany	CUIC

\*, Species used for the cladistic analyses (see text).

\*\*, Characters for *Phalera* pupae were taken from descriptions and figures in the literature. Acronyms for collections: AMNH, American Museum of Natural History, New York, NY; BMNH, The Natural History Museum, London, GB; CUIC, Cornell University Insect Collections, Ithaca, NY; INHS, Illinois Natural History Survey, Champaign, IL; NYSM, New York State Museum, Albany, NY; SJW, Susan J. Weller collection, LSU, Baton Rouge, LA; SSC, Shigero Sugi collection, Tokyo, Japan; USNM, United States National Museum, Washington, DC.

character state, while all other taxa show the second. The “primitive” character state in *Cerura/Furcula* may not be homologous with others; in both genera, the eye-piece itself is relatively small (see Fig. 7A, B).

*Front shape.* The front in pupae is defined as the sclerite to which the antennae are attached (Mosher, 1916b). There are various shapes of the front. It is smoothly rounded in most species, whereas it protrudes to varying degrees in others, *Zunacetha annulata* (Dioptinae) (Fig. 12) being an example. The front in *Datana* and *Phalera* species is highly sculpted (Fig. 13; Dolinskaya, 1989).

Some primitive Lepidoptera pupae have a “cocoon-cutter” on the head used to cut through the fabric of the cocoon, but there is no comparable structure in Ditrysia (Hinton, 1946). Various notodontids have modifications on the adult head (Miller, 1991) that assist in digging through the substrate upon emergence from the pupa. However, there seems to be no correlation between adult and pupal stages regarding modified heads. For example, notodontids with specializations in adults, such as *Thaumetopoea* and *Goacampa*, show nothing in pupae (Figs. 3, 9). In contrast, the

Table 2. Pupal characters used in a cladistic analysis of sixteen representative notodontid species. Autapomorphic characters were not used, and are omitted from the list.

1. Proximo-lateral angles of the proboscis: not reaching eye-pieces (0); reaching eye-pieces (1).
2. Labial palpus sclerite: present (0); absent (1).
3. Length of proboscis: approximately  $\frac{1}{3}$  that of wings, prothoracic legs and mesothoracic legs meeting at midline (0); approximately  $\frac{1}{2}$  that of wings, only mesothoracic legs meeting at midline (1); equal to or greater than that of wings, prothoracic and mesothoracic legs not meeting at midline (2).
4. Anterior suture of proboscis: strongly curved, arching forward toward vertex of head (1); not strongly curved and arching forward (0).
5. Antennae: shorter than mesothoracic legs (0); extending beyond mesothoracic legs (1); greatly elongate, extending to A5 (2).
6. Thorax length (ventral view): less than  $\frac{2}{3}$  total body length (0); equal to  $\frac{2}{3}$  total body length (1).
7. Secondary setae: absent (0); covering thorax and abdomen (1).
8. Dorsum of thorax: smooth or with a small ridge along midline (0); with a distinct crest along midline (1).
9. Sculpturing on caudal margin of mesothorax: not present (0); with a series of shallow depressions separated by raised ridges (1); with a series of small, quadrangular plates separated by deep pits (2).
10. Shape of mesothorax: smoothly rounded dorsally, posterior margin gradual (0); with a dorsal hump, posterior margin projecting at body midline (1).
11. Lateral portions of metathorax: roughly parallel-sided (0); sinuate (1).
12. Thoracic cuticle: smooth or with a few scattered, shallow pits (0); covered with many deep pits (1).
13. Anterior margin of each movable segment (A5–A7): unmodified (0); with a diffuse band of small pits (1); with a single row of lunate pits (2); with a distinct carina (3).
14. Abdominal cuticle: smooth or with fine wrinkles (0); with small pits scattered over the surface (1); covered with large, deep pits (2); covered with large, shallow pits and raised ridges (3).
15. Abdominal spiracles: small (0); large (1).
16. Abdominal spiracle shape: spiracle margins equal in size, spiracle opening laterally (0); anterior spiracular margin more robust and raised, so that spiracle opens posteriorly (1).
17. Segments A8–A10: tapered posteriorly (0); broadly rounded (1).
18. Antero-dorsal margin of A10: unmodified (0); with a deep furrow (1); sharply elevated, with a lip-shaped edge (2).
19. Dorsum of A10: smooth (0); with a raised, reticulate area anterior to cremaster (1); with numerous, small longitudinal ridges (2).
20. Cremaster: variously shaped (0); bifurcate (1); long and spine-like (2); broad, compressed (3); absent (4).
21. Base of cremaster: smooth (0); fluted (1).
22. Number of cremaster setae: 20 or more (0); between eight and ten (1); setae absent (2); cremaster absent (?).
23. Body: cylindrical (0); dorso-ventrally compressed (1).
24. Body: variously shaped, but roughly elongate (0); wide relative to its length (1).

Table 3. Data matrix of 24 pupal characters (Table 2) for 16 species of Notodontidae (see Table 1) with *Doa ampla* used as an outgroup.

	5	10	15	20	24
<i>Doa</i>	00000	00000	00000	00000	0000
<i>Thaumetopoea</i>	01000	01000	00000	00001	0201
<i>Closteria</i>	00000	01000	10011	00002	0000
<i>Platychasma</i>	10201	00000	10010	00020	0000
<i>Notodontia</i>	11100	00000	10011	01001	0100
<i>Furcula</i>	11000	00000	10011	01004	0?11
<i>Gluphisia</i>	11000	00000	10011	01004	0?11
<i>Datana</i>	11100	01000	10021	00101	0200
<i>Phalera</i>	11100	01000	10021	00101	0200
<i>Goacampa</i>	11210	00110	10331	00000	0100
<i>Crinodes</i>	11210	00110	10311	00201	0100
<i>Heterocampa</i>	11211	00020	10111	00011	0200
<i>Lochmaeus</i>	11211	00020	10111	00011	0200
<i>Symmerista</i>	10211	00000	11211	10001	1100
<i>Didugua</i>	10211	00000	11211	10001	1100
<i>Josia</i>	11212	10001	10010	10003	1100
<i>Zunacetha</i>	10212	10001	10010	10003	1100

head of *Z. annulata* has a tubercle in the pupal stage (Fig. 12) but is unmodified in adults.

*Labial palpi.* (2) Although the labial palpi can be relatively large in taxa outside the Notodontidae (e.g., *Doa ampla*, Fig. 2A), they are either highly reduced or absent among notodontids (Mosher, 1916b, 1918b; Common, 1990; Minet, 1991). Most commonly they are absent, but a small, triangular labial palpus sclerite occurs among various notodontid subfamilies (Dolinskaya, 1989) including the Platychasmatinae (Fig. 5A), Nystaleinae (Fig. 11A), and Dioptinae (Fig. 12A).

It is interesting that, contrary to modern ideas, Mosher's concept of the Noctuoidea excluded the Notodontidae. She placed notodontids in a separate superfamily, the Notodontoidea, along with the Geometridae. Unfortunately, there is still no pupal character known, comparable to the metathoracic tympanum in adults, that can be used to define the Noctuoidea (as the term is currently applied). Mosher (1916b, 1918b) grouped the Notodontidae and Geometridae together because in both the pupae lack labial palpi, but instead have only "a very small triangular or polygonal area" (1916b:125) remaining. Adult and larval data certainly do not support Mosher's phylogenetic hypothesis (see Miller, 1991; Minet, 1991).

*Length of proboscis.* (3) Mosher (1916b) used the term maxillae for the proboscis of Common (1990); I follow the latter. Both authors noted that, although highly variable in length, the proboscis is always visible in Lepidoptera. In notodontids, extremes range from the thaumetopoeines, where the proboscis is less than  $\frac{1}{3}$  the length of the mesothoracic wings (Fig. 3A), to the Dioptinae, where it can extend beyond the caudal margin of the wings, actually touching A5 (Fig. 12A). I divided the character into three states (Table 2). In species with an extremely short proboscis,

the prothoracic and mesothoracic legs meet at the ventral midline (Figs. 3A, 4A, 7A, 8A). In taxa such as *Datana* and *Notodonta*, with a tongue only slightly shorter than the thorax, the mesothoracic legs meet at the midline but the prothoracic ones do not (Fig. 6A; Mosher, 1918b). Finally, in long-tongued species (Figs. 5A, 9A–12A) neither pairs of legs meet along the midline (Mosher, 1918b; Dolinskaya, 1989).

This character has been noted by all authors since Packard (1895). However, proboscis length in pupae can vary greatly even within notodontid subfamilies. For example, there are heterocampine species in which the tongue is as long as the wings (Fig. 10A), and species where the proboscis is much shorter than the wings. Similar variation occurs in the Nystaleinae. It is not surprising that tongue length in pupae is correlated with that in adults (Poulton, 1891).

*Anterior sutures of proboscis.* (4) I here define the “anterior sutures” of the proboscis as the sutures where the base of the proboscis and the head join (see Figs. 10, 11). In most species, these either arch slightly forward at their midpoint (Fig. 3A), or are straight with an orientation essentially perpendicular to the body midline (Fig. 8A). Four subfamilies of the Notodontidae—the Dudusinae, Heterocampinae, Nystaleinae, and Dioptinae—exhibit a different configuration. In these, the anterior sutures of the proboscis are strongly curved, bending toward the vertex of the head, with the proximo-medial angles of the proboscis being narrow (Figs. 9A–12A).

*Length of antennae.* (5) Like the proboscis, the antennae of pupae vary in length. In addition, the antennae can either be shorter than the mesothoracic legs or they can extend beyond the mesothoracic legs. The former is typical of most notodontids (e.g., Fig. 9A) as well as their sister group, *Doa* (Fig. 2A), while the latter appears to be restricted to the Platychasmatinae (Fig. 5A), Heterocampinae (Fig. 10A), Nystaleinae (Fig. 11A) and Dioptinae (Fig. 12A). Mosher (1916b), based on study of *Phryganidia californica*, listed long antennae, touching A5, as a diagnostic trait for the Dioptinae. This character state occurs in all the dioptines I examined.

### Thorax:

*Thorax length.* (6) Dioptinae are unusual in that the thorax is elongate. In the species I studied, the thorax is  $\frac{2}{3}$  the total body length (Fig. 12), whereas in other notodontids the thorax is less than  $\frac{2}{3}$  the body length (e.g., Figs. 3, 5, 10).

*Secondary setae.* (7) There are primary setae on the body in pupae analogous to the primary setae in larvae (Common, 1990). Those of pupae are small and difficult to locate (Mosher, 1916b). The primary setae of *Zunacetha annulata* (Fig. 12) are large compared to the other species I examined; usually they are microscopic. I did

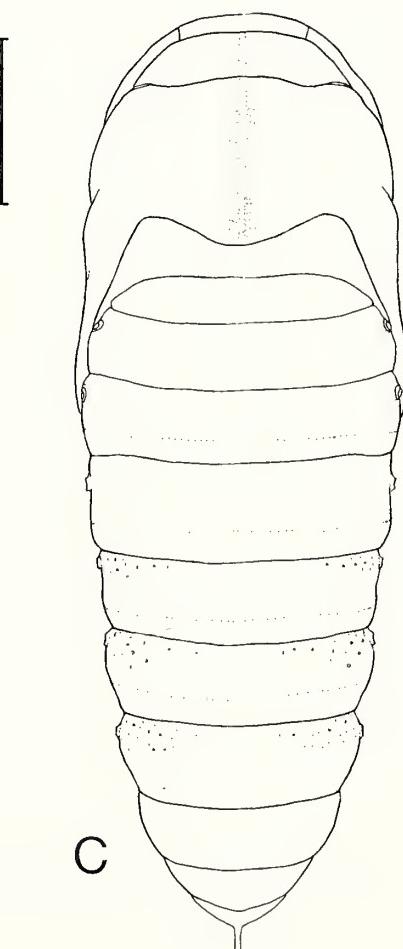
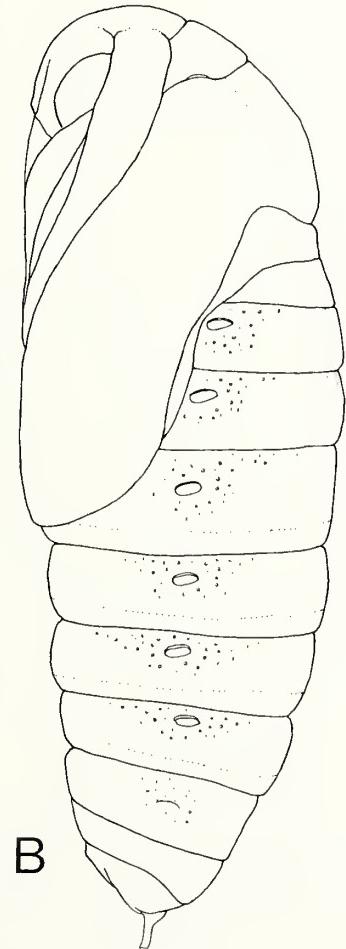
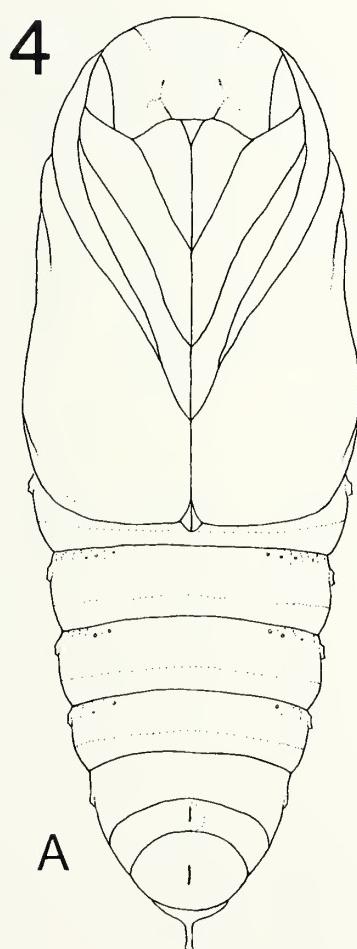
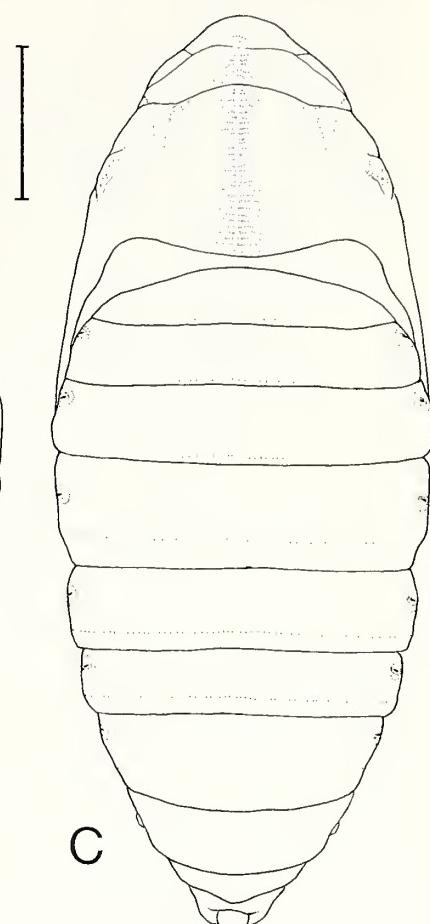
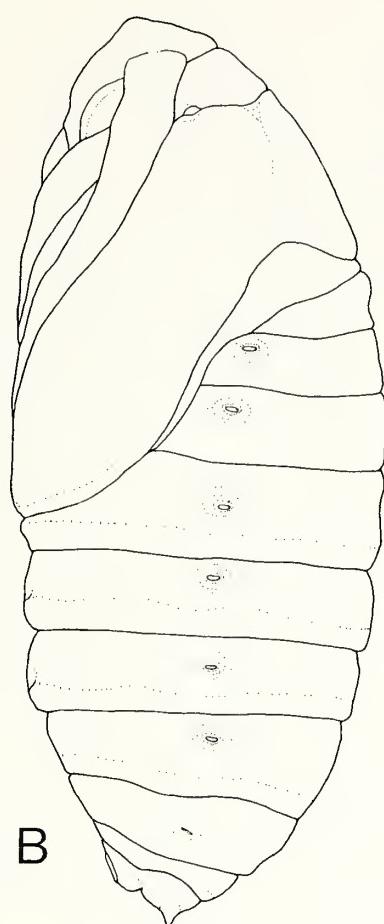
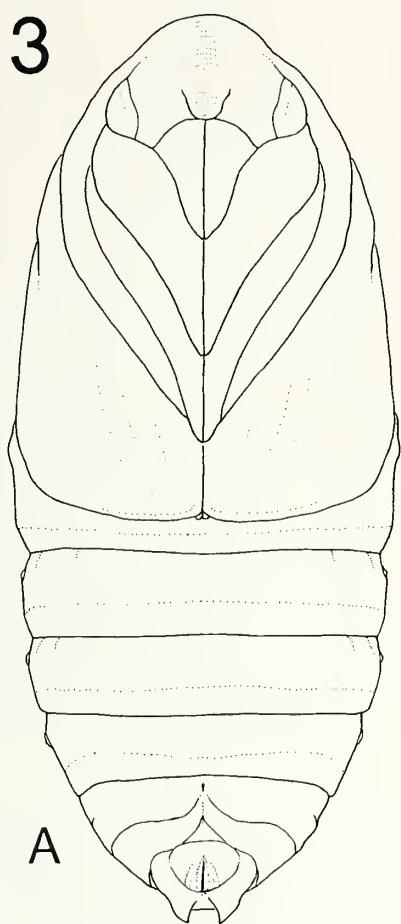
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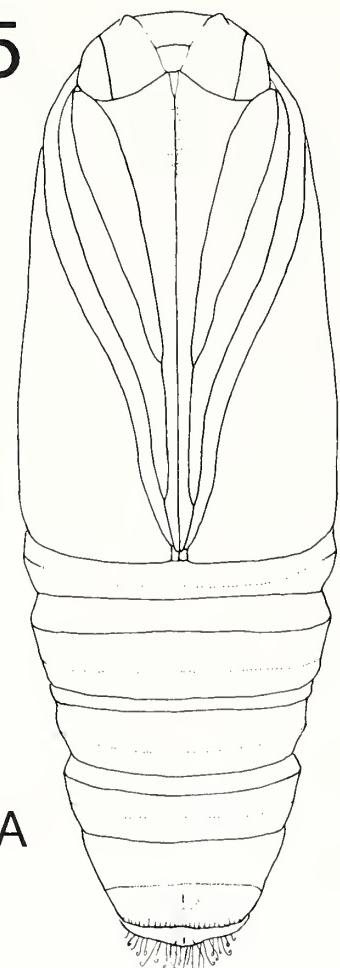
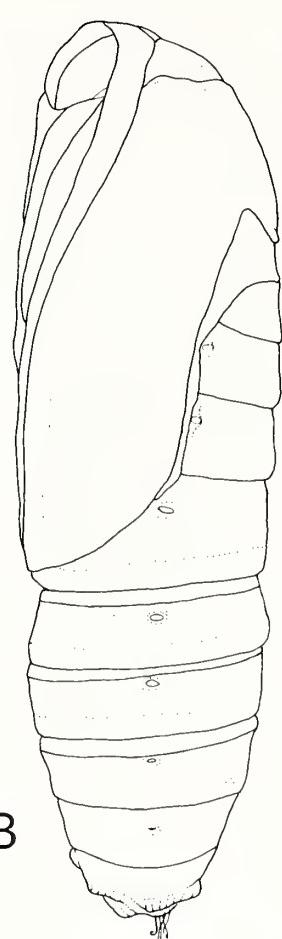
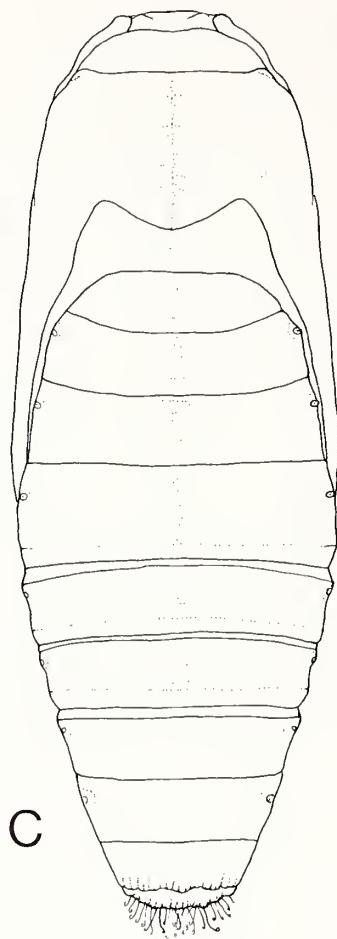
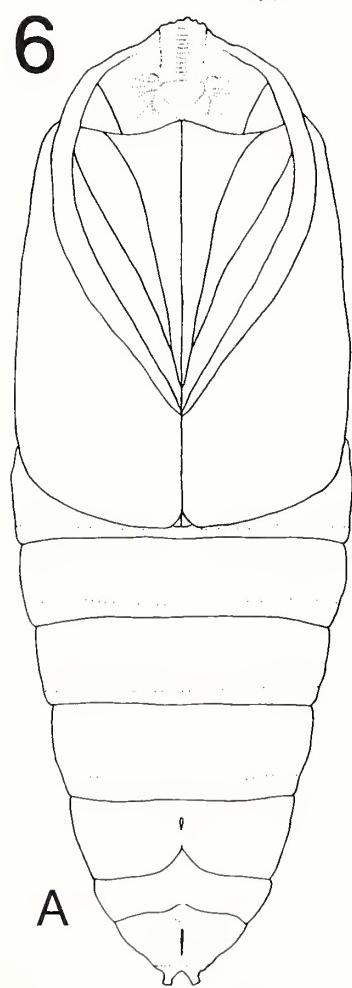
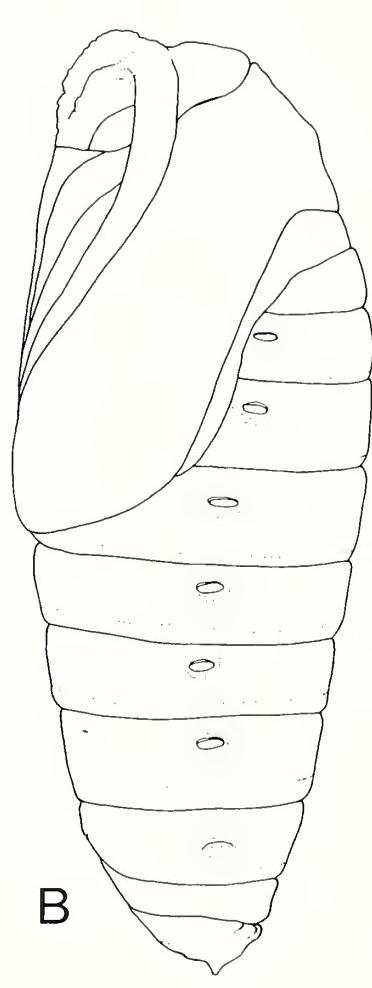
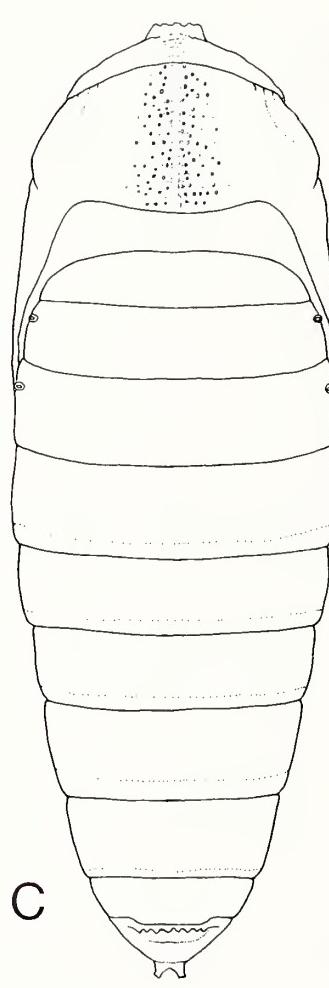
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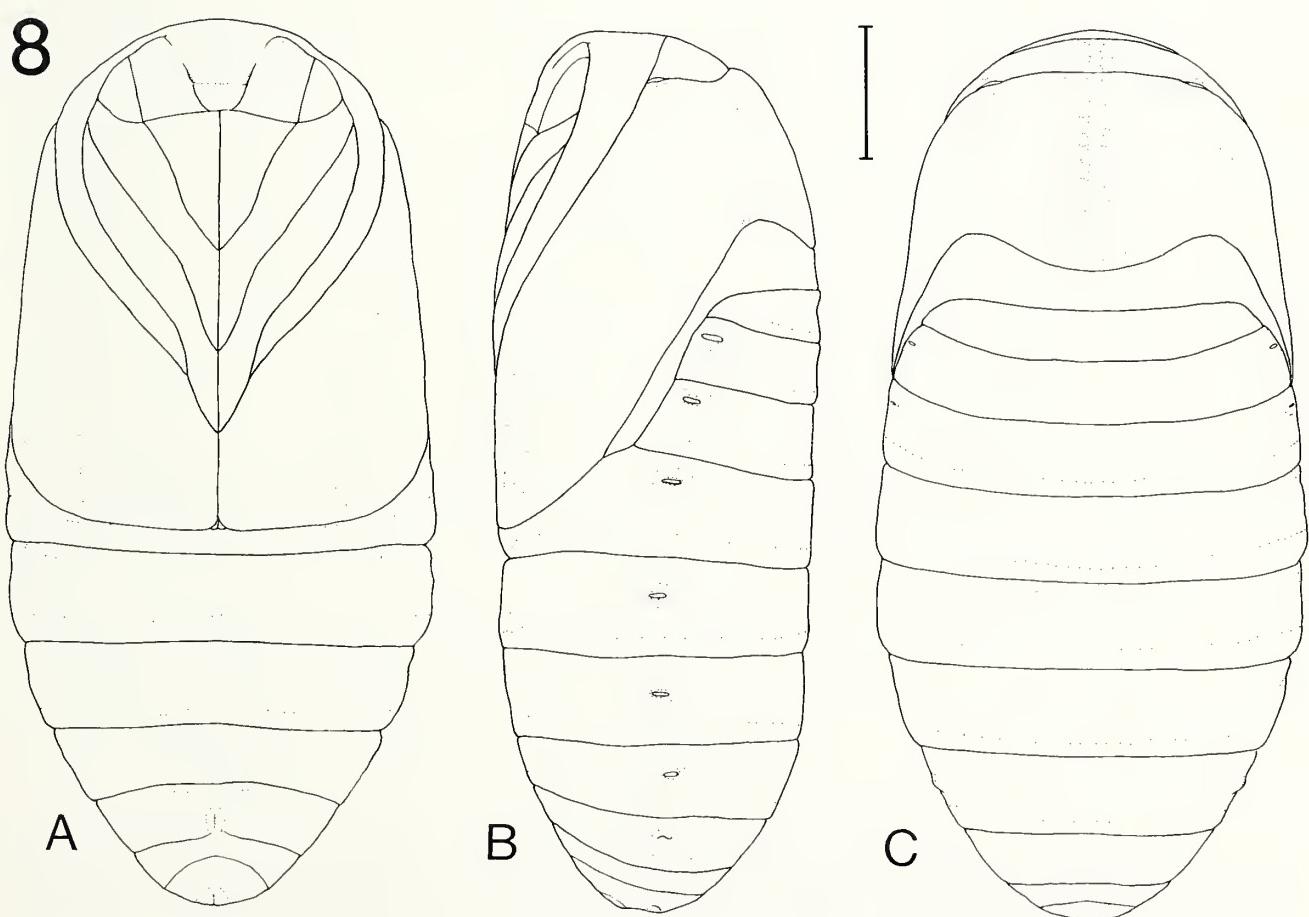
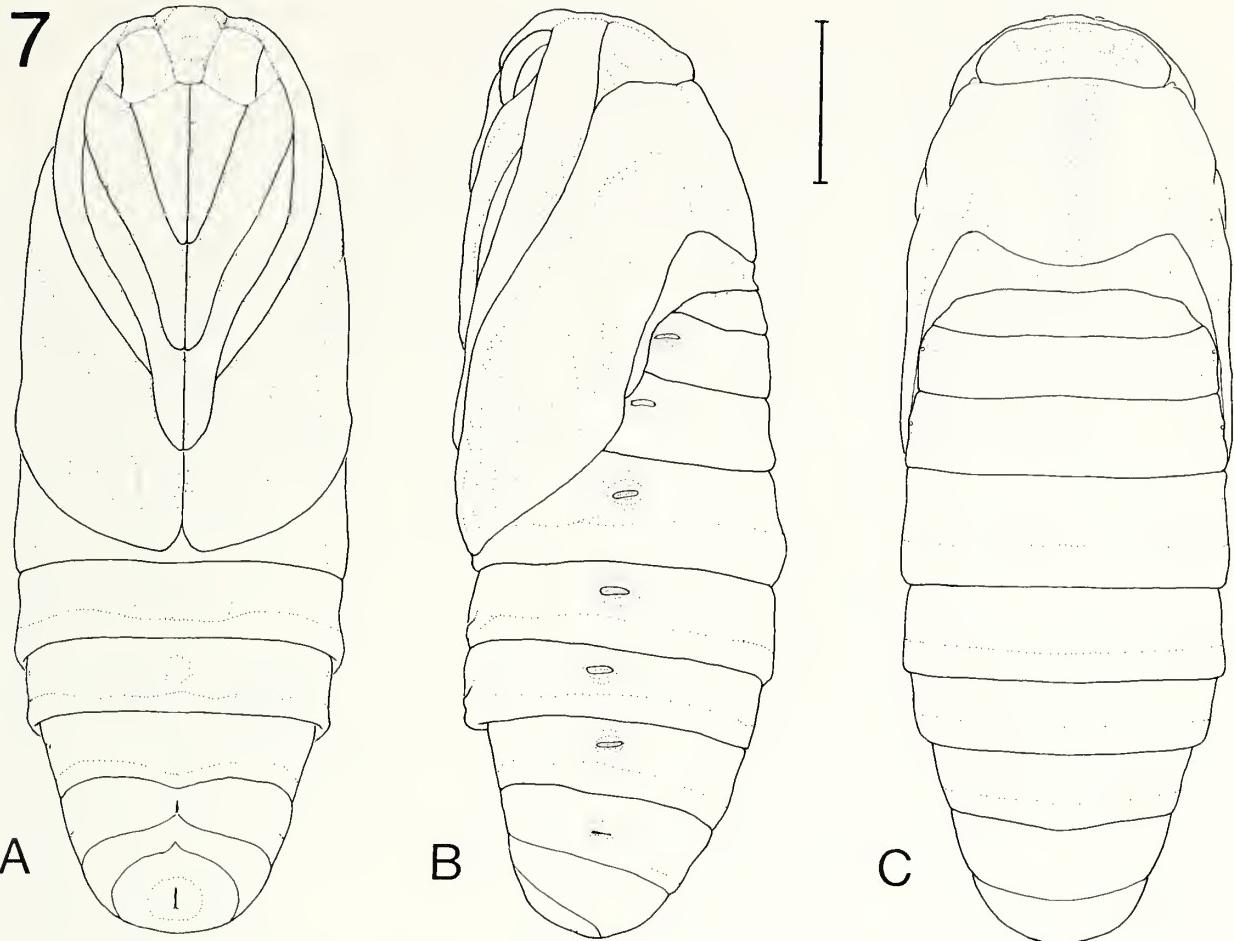
Figs. 3, 4. Pupae of Notodontidae. 3. *Thaumetopoea pinivora* (Treitschke). 4. *Closteria albosigma* Fitch. A. Ventral view. B. Lateral view. C. Dorsal view. Scale lines = 3 mm.

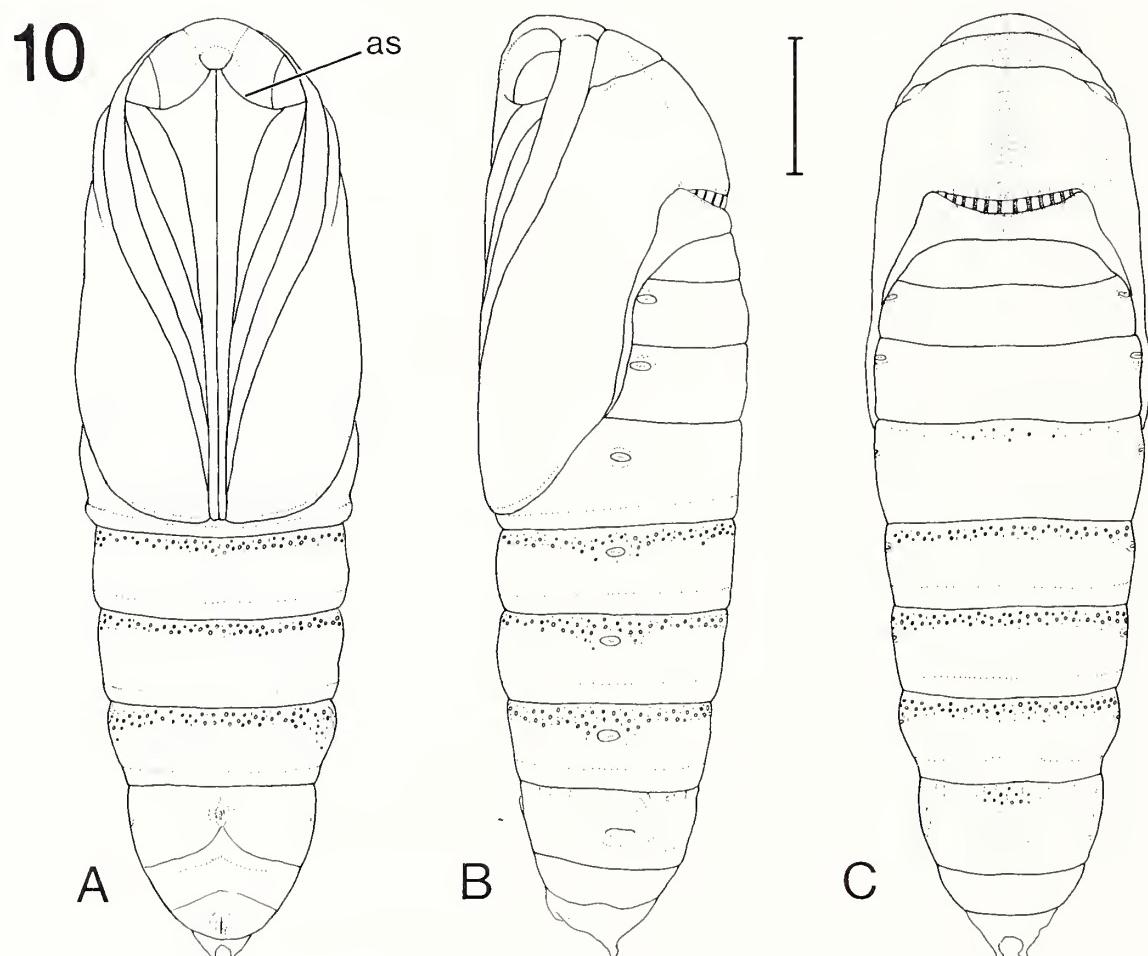
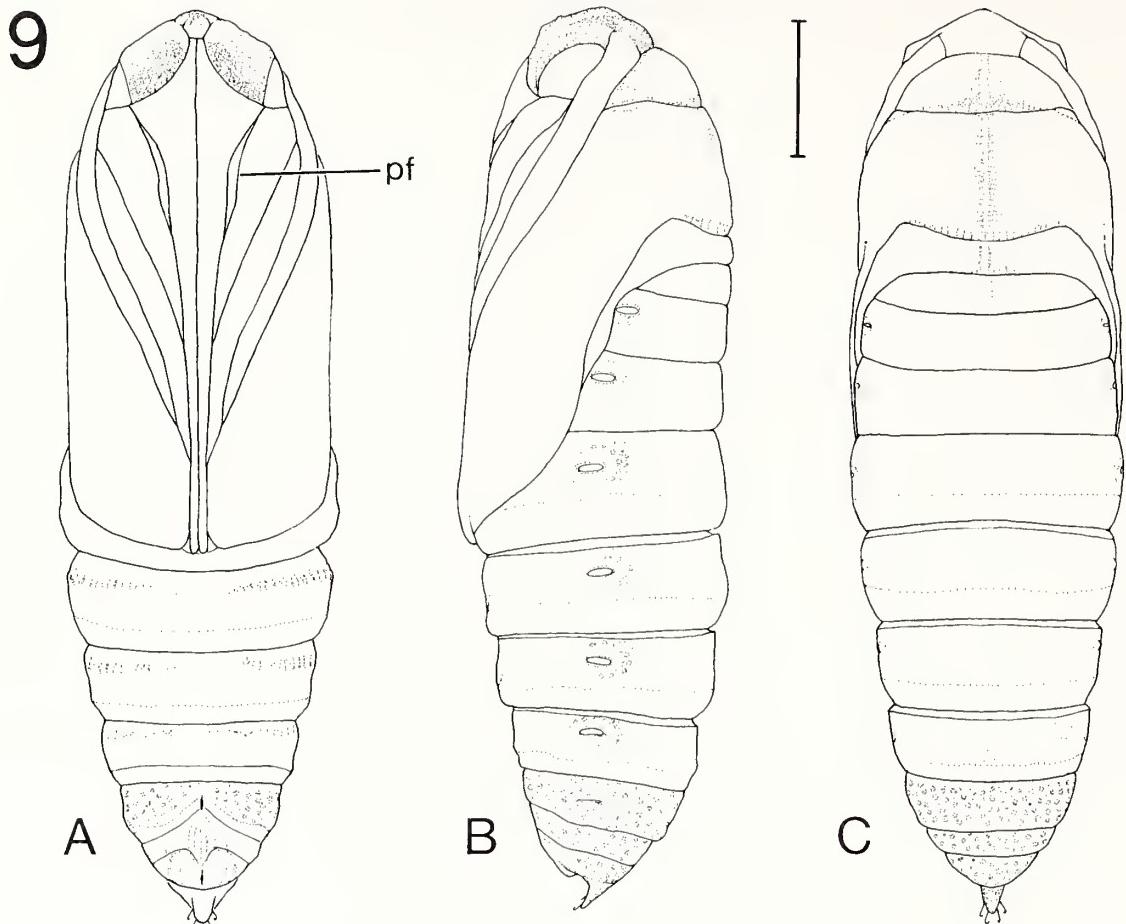
Figs. 5, 6. Pupae of Notodontidae. 5. *Platychasma virgo* Butler. 6. *Datana robusta* Strecker. A. Ventral view. B. Lateral view. C. Dorsal view. Scale lines = 3 mm.

Figs. 7, 8. Pupae of Notodontidae. 7. *Furcula scolopendrina* (Boisduval). Scale line = 3 mm. 8. *Glaphisia septentrionis* Walker. Scale line = 2 mm. A. Ventral view. B. Lateral view. C. Dorsal view.



**5****A****B****C****6****A****B****C**





Figs. 9, 10. Pupae of Notodontidae. 9. *Goacampa variabilis* Schaus. 10. *Lochmaeus manteo* Doubleday. A. Ventral view. B. Lateral view. C. Dorsal view. as = anterior suture; pf = femur of prothoracic leg. Scale lines = 3 mm.

not examine primary setal patterns in pupae, but such research might be valuable. They have rarely been used for taxonomic purposes.

Secondary setae can also occur. For example, larvae and pupae of Lymantriidae are covered with long secondary setae (Poulton, 1891; Nakamura, 1976). The relationship between presence or absence of secondary setae in the larval and pupal stages of Notodontidae is interesting. This character shows a high level of homoplasy in larvae; secondary setae occur in caterpillars of the Thaumetopoeinae, Pygaerinae, Phalerinae, Nystaleinae, Dioptinae, and Dudusinae, and each of these cases is thought to have evolved separately (Miller, 1991). Presence of secondary setae in the pupal stage appears to exhibit a more restricted taxonomic distribution. Genera such as *Cyanotricha* (Dioptinae) and *Dasylophia* (Nystaleinae) have secondary setae in larvae but not in pupae. Based on the notodontid pupae I examined, secondary setae occur only in the subfamilies Thaumetopoeinae, Pygaerinae, and Phalerinae. Undoubtedly, examples in other subfamilies will eventually be found. Secondary setae in notodontid pupae are extremely short, almost microscopic (Mosher, 1918b).

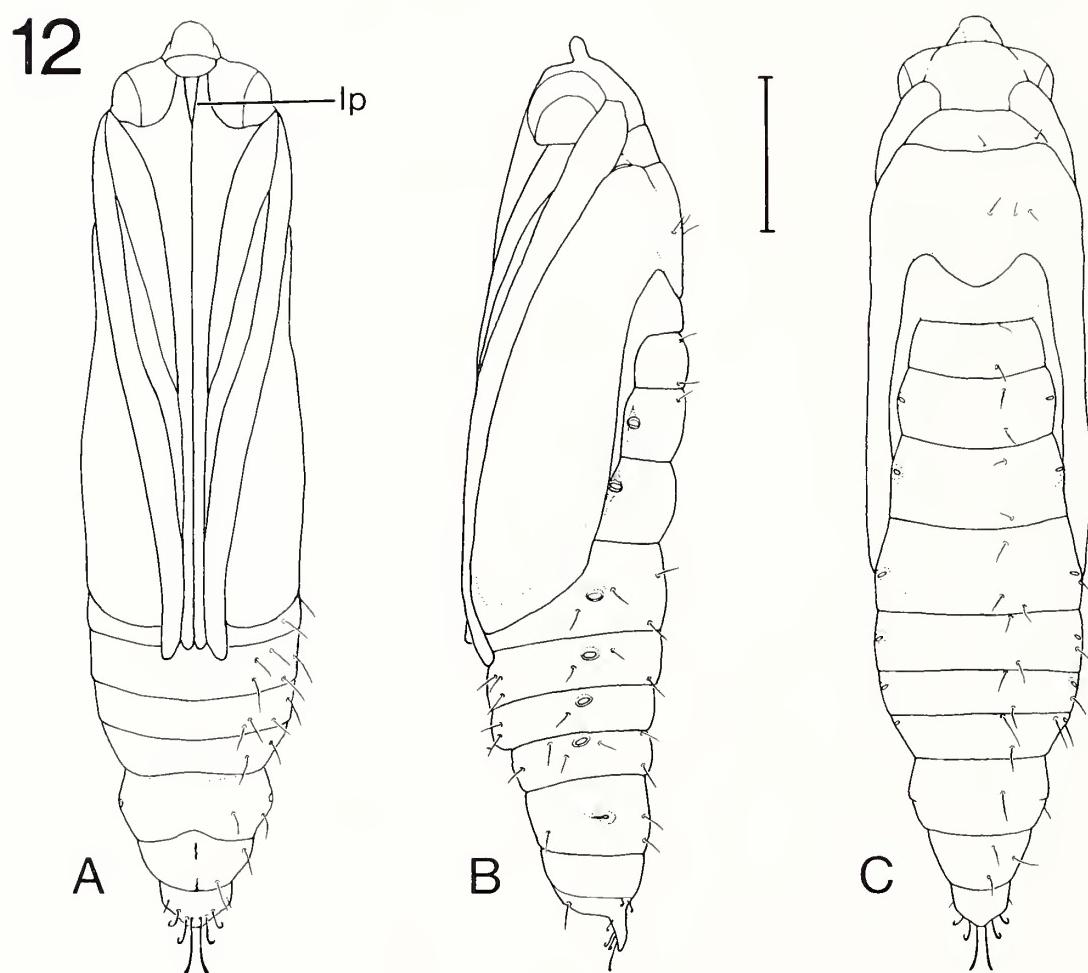
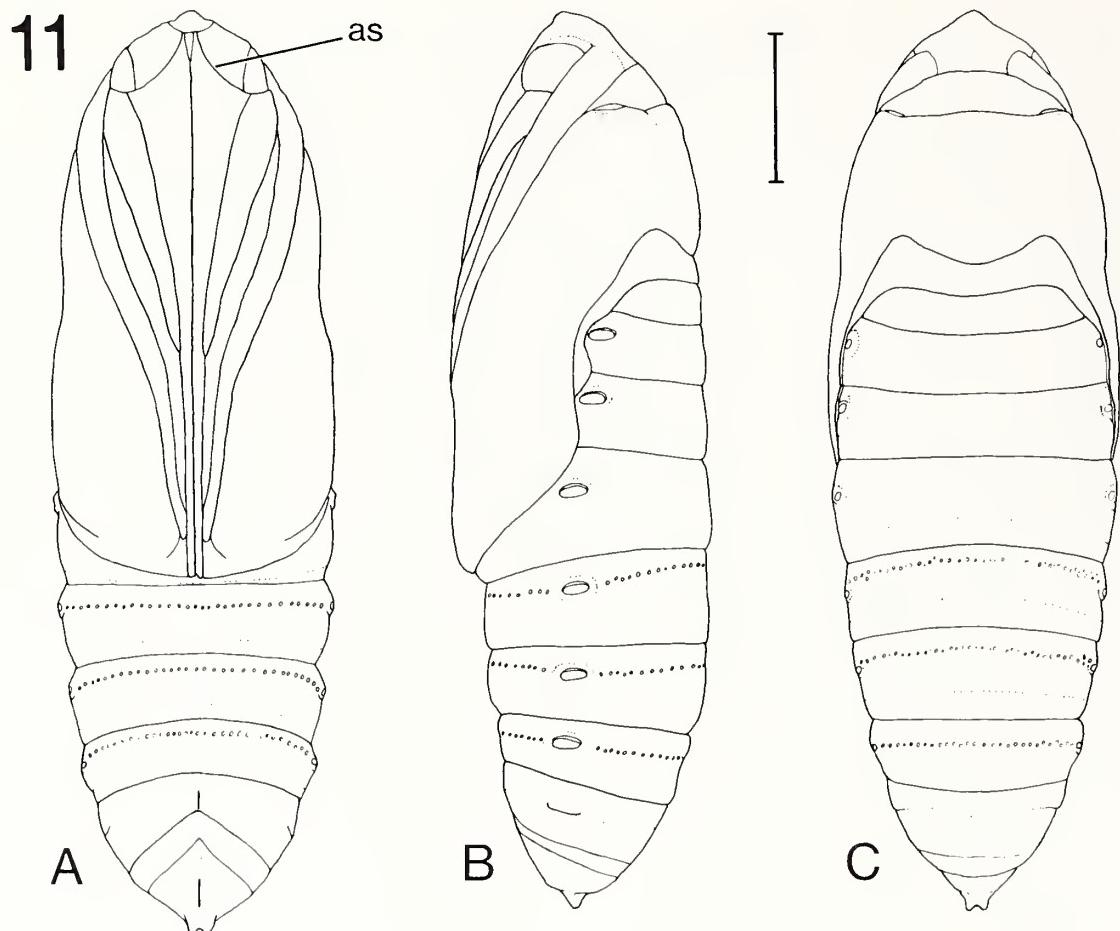
*Femur of prothoracic legs.* Both Common (1990) and Mosher (1918b), in their diagnoses for the family, stated that the femur of the prothoracic leg is never visible in pupae of Notodontidae. The structure is frequently visible in various other families. I found that the profemur can be seen in at least one notodontid species, *Goacampa variabilis* (Dudusinae) (Fig. 9A). This is obviously a derived character state for the Notodontidae, but without examining additional species its usefulness for phylogeny is unknown.

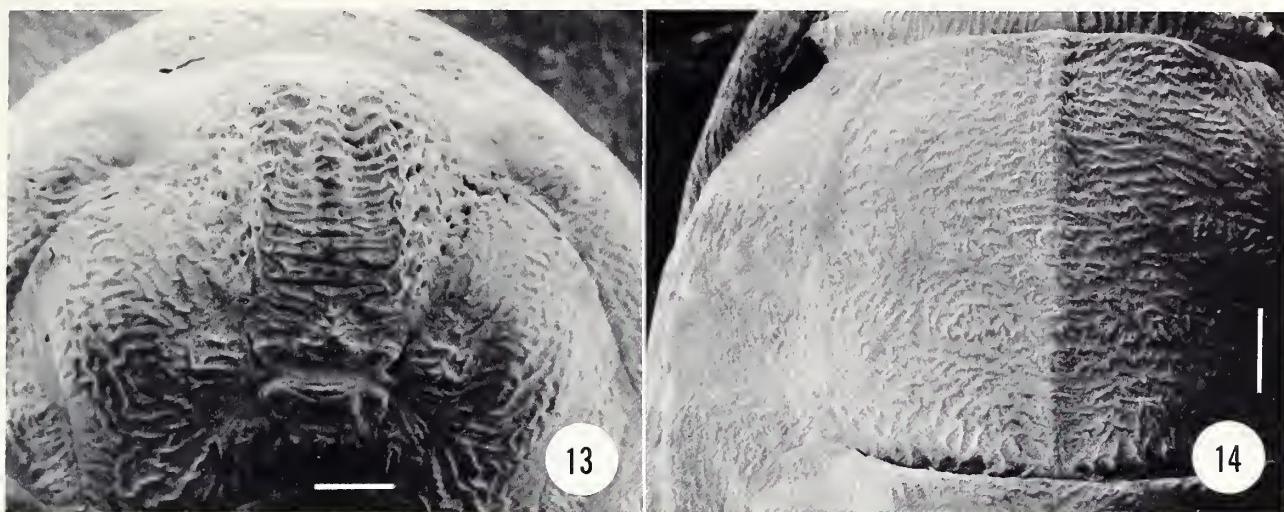
*Prothoracic crest.* (8) In the two dudusines I studied, *Crinodes besckei* and *Goacampa variabilis*, there is a distinct crest along the midline on the dorsum of the mesothorax (Fig. 14). It is present, but less obvious, on the prothorax as well. Although a few other taxa show a slightly raised area along the midline (e.g., Figs. 3C, 10C), it is not pronounced.

*Mesothoracic spiracle.* The shape of the mesothoracic spiracle varies among species (Mosher, 1916b), with sculpturing around the spiracle showing the most significant differences. Unfortunately, thorough study would require SEM for all taxa, something beyond the scope of this paper.

*Pits on mesothoracic caudal margin.* (9) On the dorsum of the pupa some taxa exhibit modifications of the mesothoracic caudal margin. The most remarkable of these occurs in the Heterocampinae (Fig. 10C). Here, there is a row of from six to twelve small, quadrangular plates separated by deep pits (Figs. 15–17). The plates are slightly convex (Fig. 16) and their surfaces are rugose under high magnification (Fig. 18). This apomorphy, first mentioned by Dyar (1889) and described by Packard (1895) in species of North American Heterocampinae, has been noted by most subsequent authors. Based on my study and on reports in the literature, the trait is restricted to Heterocampinae but is quite widespread within the subfamily, occurring in at least nine genera (Dyar, 1889; Packard, 1895; Mosher, 1916b, 1918b; Weller, 1987; Dolinskaya, 1989). Its function is unknown.

A similar, but less spectacular, modification can be found in *Goacampa variabilis* and *Crinodes besckei* (both Dudusinae). In these species, the caudal margin of the mesothorax bears a row of shallow depressions separated by raised longitudinal ridges (Figs. 9C, 14). Although the character in Heterocampinae and Dudusinae may be homologous, the character states in the two groups are clearly separable.





Figs. 13, 14. Scanning electron micrographs of notodontid pupae. 13. Front of *Datana ministra* (Drury), ventral view (500  $\mu\text{m}$ ). 14. Meso- and metathorax of *Goacampa variabilis* Schaus, dorsal view with anterior at top (500  $\mu\text{m}$ ). Scale lengths in parentheses.

*Shape of mesothoracic caudal margin.* (10) A modification of the mesothoracic caudal margin, not related to sculpturing, occurs in pupae of Dioptinae. Here, the mesothorax is humped posteriorly and its caudal margin projects sharply posteriad at the body midline (Fig. 12C; Mosher, 1916b). In other notodontids, the caudal margin of the mesothorax forms a shallow curve posteriorly (e.g., Fig. 11C). The derived state seems to provide yet another synapomorphy for the Dioptinae.

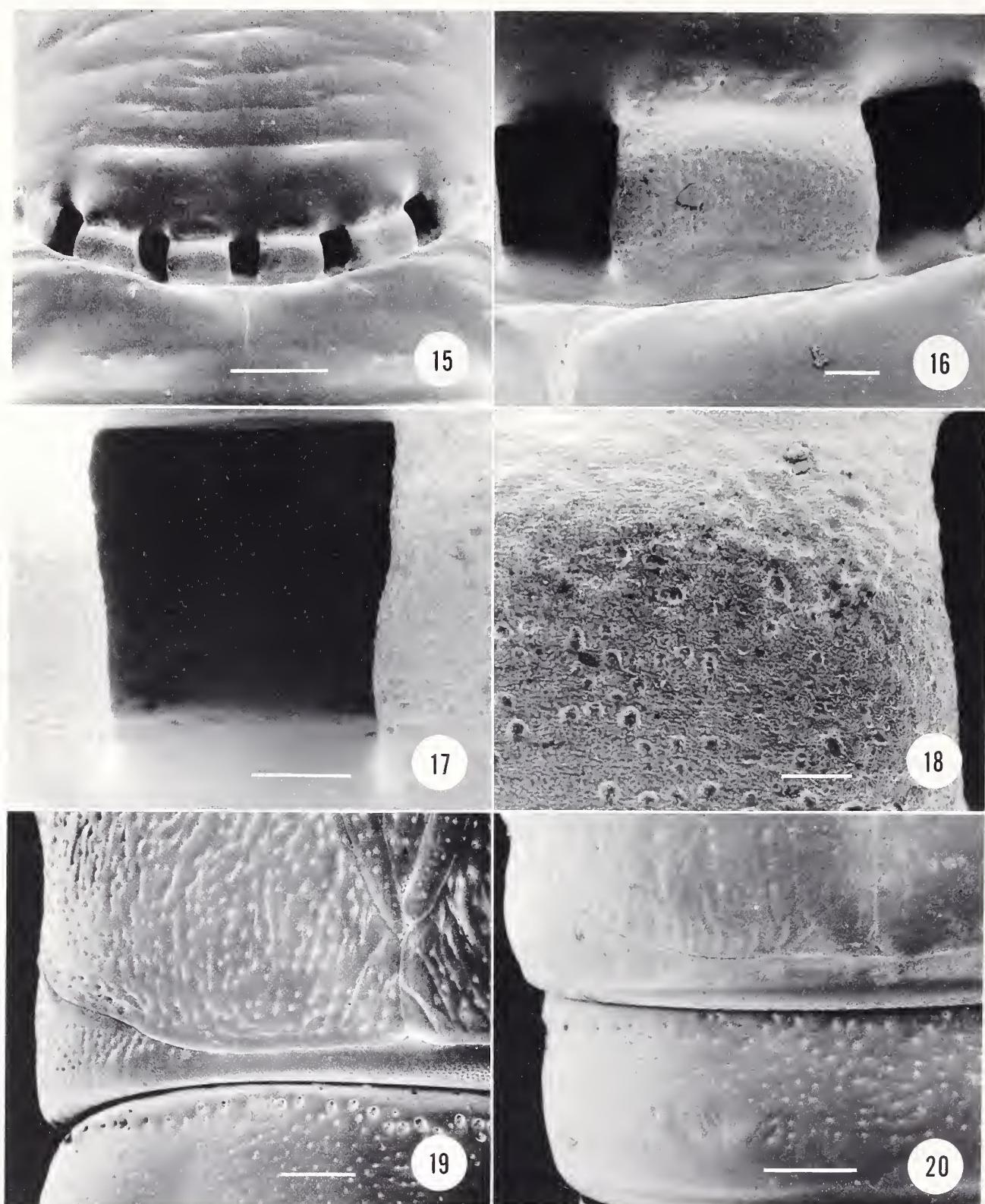
*Lateral extensions of metathorax sinuate.* (11) In all pupae I studied except *Doa ampla* and *Thaumetopoea pinivora*, the lateral extensions of the metathorax have a constriction opposite the A2 spiracle and an expanded distal portion (e.g., Figs. 9B, 11B). This configuration is more marked in some taxa than in others, but it seems to define a monophyletic group that includes all notodontid subfamilies except the Thaumetopoeinae.

The length of the lateral portions of the metathorax also varies among Notodontidae. In some species they extend as far posteriad as A4, either touching the anterior margin of that segment (e.g., *Thaumetopoea pinivora*, Fig. 3B) or extending beyond it (e.g., *Platychasma virgo*, Fig. 5B). In other taxa, they extend only as far as the middle of A3 (e.g., *Goacampa variabilis*, Fig. 9B). However, this character shows so much homoplasy that its value is questionable.

*Forewing venation.* In most Ditrysia, the only wings visible in the pupa are the forewings (Mosher, 1916b). The trifid Noctuoidea, to which the Doidae and Notodontidae belong (Miller, 1991), have the forewing cubital vein three-branched (comprising veins CuA<sub>1</sub>, CuA<sub>2</sub>, and M<sub>3</sub>), a plesiomorphic trait. The derived state is the quadrifid condition, where M<sub>2</sub> branches from the cubital as well. These veins are usually difficult to see in pupae, except during later development when the pharate

←

Figs. 11, 12. Pupae of Notodontidae. 11. *Didugua argentininea* Druce. Scale line = 3 mm. 12. *Zunacetha annulata* Guérin. Scale line = 2 mm. as = anterior suture; lp = labial palpi. A. Ventral view. B. Lateral view. C. Dorsal view.



Figs. 15–20. Scanning electron micrographs of notodontid pupae. 15. Posterior margin of mesothorax in *Heterocampa guttivitta* Walker, dorsal view (400  $\mu\text{m}$ ). 16. A single plate from the structure in Figure 15 (50  $\mu\text{m}$ ). 17. A pit between plates (40  $\mu\text{m}$ ). 18. Surface structure of a single plate (20  $\mu\text{m}$ ). 19. *Symmerista leucitys* Franclemont ventral view, showing bottom of wing and segments A4–A5 on right side; tips of antennae in upper right (500  $\mu\text{m}$ ). 20. Similar view of *Ellida caniplaga* (500  $\mu\text{m}$ ). Scale lengths in parentheses.

adult can be seen through the pupal cuticle. Nevertheless, the trifid condition can be used to separate pupae of the Doidae and Notodontidae from other Noctuoidea. There is one exception; the subfamily Platychasmatinae, containing the monobasic genus *Platychasma*, is the only notodontid group in which the forewing is quadrifid (Nakamura, 1956; Miller, 1991).

*Cuticle surface structure.* (12) Thoracic surface structure seems to vary independently of that on the abdomen. The nystaleine pupae I examined are characterized by numerous, deep pits covering the thorax (Fig. 19). The thorax of other notodontids either has a few shallow pits scattered over its surface (e.g., *Ellida caniplaga*; Fig. 20), or is smooth.

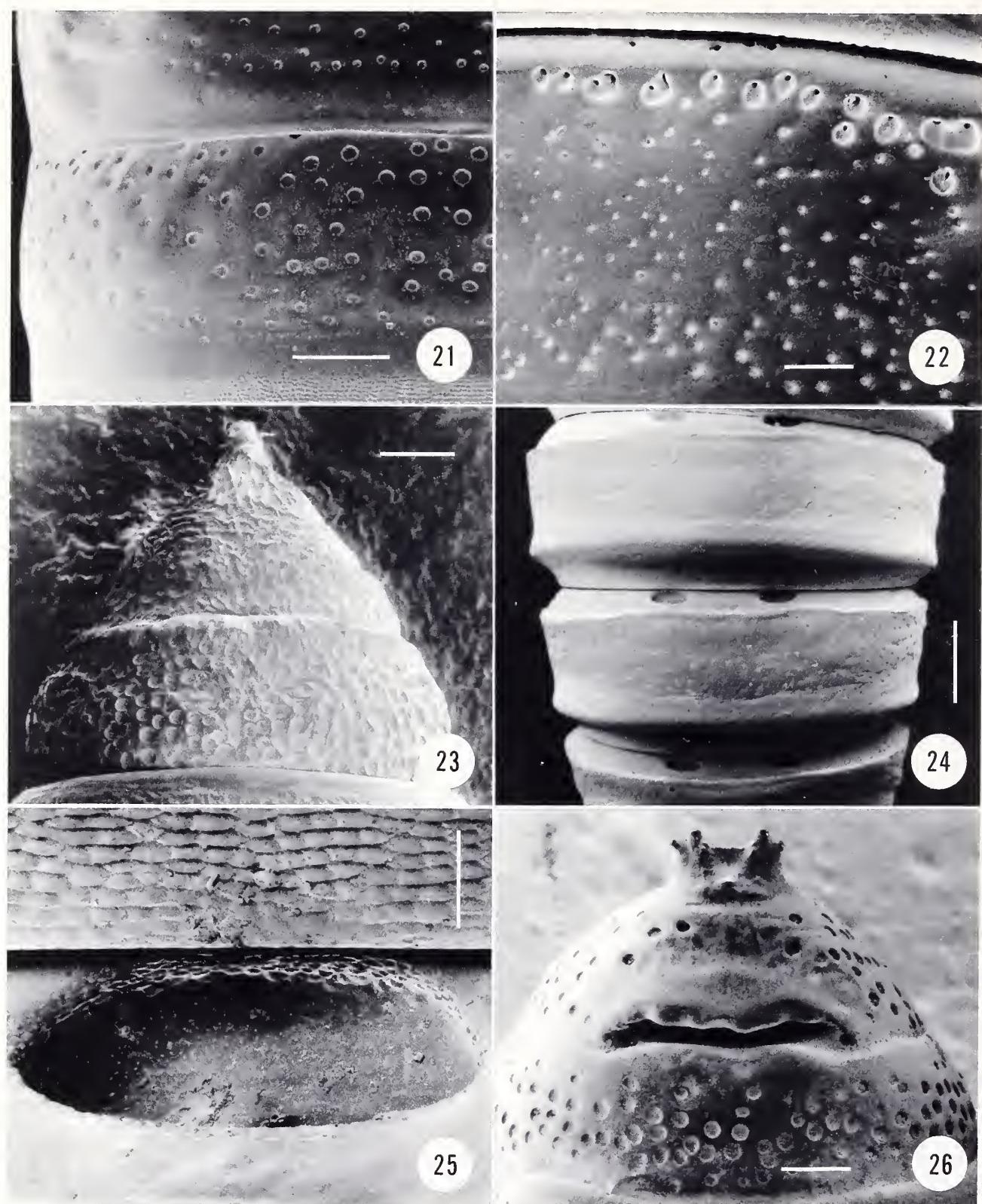
*Appendages standing out in relief.* In most notodontid pupae the appendages are fused together to form a relatively flat surface. In *Cerura* and *Furcula*, the proboscis, legs, and antennae stand out in relief from the body surface (Mosher, 1916b), a character state also noted by Dolinskaya (1989) for the Palearctic genera *Harpyia* and *Ptilophora*. I placed *Ptilophora* in the subfamily Notodontinae along with *Cerura* and *Furcula*, but I put *Harpyia* in the Heterocampinae (Miller, 1991). The derived state is not found in other Notodontinae, such as *Gluphisia* and *Notodonta* (Dolinskaya, 1989). This trait needs further study.

#### Abdomen:

*The movable segments (A5–A7).* (13) In primitive Lepidoptera, abdominal segments A1–A7 are movable, while A8–A10 are always fused (Mosher, 1916b). In more advanced families, such as the Notodontidae, the only movable segments of the abdomen are A5–A7 (Mosher, 1918b). Segments A1–A4 show little morphological variation among notodontid species. The movable segments, on the other hand, often exhibit unique structural modifications not found on other abdominal segments. Segments A9 and A10, bearing the cremaster, show extreme variability (see Character 20).

Various types of specializations can be found along the anterior margin of the movable segments in Notodontidae. The traits appear to provide valuable phylogenetic information, especially useful at the subfamily level. Among more primitive notodontid subfamilies, the movable segments are not modified (e.g., Figs. 3, 7, 8). In advanced groups, however, at least four discrete character states occur: Heterocampine pupae have a diffuse band of small pits ringing the anterior margin of each movable segment (Figs. 10, 21). Nystaleine pupae have a single row of lunate pits (Figs. 11, 22). Mosher (1918b) first described this trait for *Symmerista*, but it occurs in other Nystaleinae as well. Finally, in Dudusinae there is a sharp carina near the anterior margin of each movable segment (Fig. 9). A similar carina can be found in *Hypereschra georgica* (Fig. 24). This species has long been placed in the subfamily Notodontinae (Packard, 1895). If that placement is correct, the carina has evolved there independently.

*Cuticle structure.* (14) Various authors have characterized the abdomen in Notodontidae as being punctate (Mosher, 1918b; Marumo, 1920; Common, 1990). I did not survey abdominal surface structure in detail, but there is considerable variation among species. The cuticle surface of *Doa ampla* and *Thaumetopoea pinivora* is smooth or somewhat wrinkled, without punctations. In other groups, small punctations are the general rule (Figs. 19–22), but in *Datana* and *Phalera* (both Phalerinae),



Figs. 21–26. Scanning electron micrographs of notodontid pupae. 21. Segment A4 of *Heterocampa guttivitta* Walker, dorsal view with anterior at top (500  $\mu\text{m}$ ). 22. Segment A5 of *Symmerista leucitys* Franclemont, ventral view with anterior at top (200  $\mu\text{m}$ ). 23. Terminal segments of *Goacampa variabilis* Schaus, dorsal view with posterior at top (500  $\mu\text{m}$ ). 24. Segments A4–A7 of *Hyperaeschra georgica* Herrich-Schäffer, dorsal view with anterior at top, showing paired pits (1 mm). 25. A single pit on A6 of *H. georgica* (100  $\mu\text{m}$ ). 26. Segments A8–A10 of *Datana ministra* (Drury), dorsal view with posterior at top, showing furrow on A10 (500  $\mu\text{m}$ ). Scale lengths in parentheses.

the abdomen is covered with large pits (Fig. 26; Dyar, 1891; Dolinskaya, 1989). The abdomen of *Goacampa variabilis* exhibits complex surface sculpturing, with shallow pits and furrows (Fig. 23). This character shows variation analogous to that on the surface of the larval head (see Miller, 1991). Like that character, SEM study across a wide variety of species would be valuable.

*Paired pits on A5–A7.* In *Hyperaeschra georgica*, there is a pair of large dorsal pits on the anterior margin of A5–A7 (Figs. 24, 25). The character is distinctive, but I observed it only in this species. I have not seen reference to these structures in the literature, and their function is unknown.

*Spiracle size.* (15) The abdominal spiracles are found laterally on segments A2–A8 (Fig. 2B). The one on A8 is always smaller than others, and according to Mosher (1916b) it is not functional. The abdominal spiracles show size variation across taxa. I simply scored them as being either large or small; a more detailed analysis is needed. Small spiracles occur in Doidae, Thaumetopoeinae, Platychasmatinae, and Dioptinae (Figs. 2B, 3B, 5B, 12B).

*Spiracle shape.* (16) I used one character involving spiracle shape. In Dioptinae and Nystaleinae, the anterior margin of each abdominal spiracle is more robust and heavily sclerotized. Furthermore, this margin is raised so that the spiracular opening faces somewhat posteriorly rather than laterally, the typical orientation.

There are also differences in the sculpturing around the spiracle (Mosher, 1918b). For example, some species have the entire spiracle raised from the body surface (Fig. 2A). This is yet another character that would benefit from comprehensive SEM study.

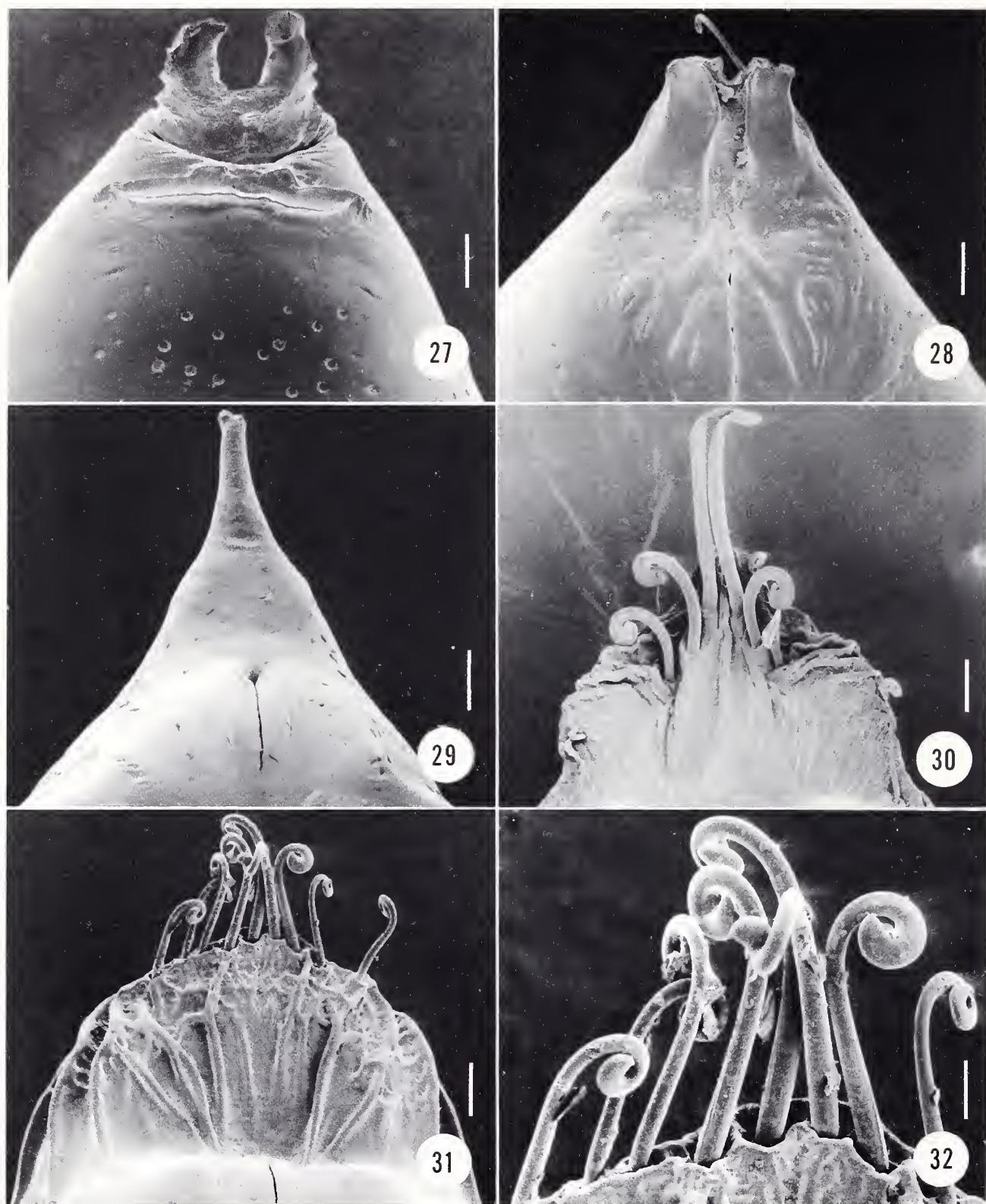
*Shape of segments A8–A10.* (17) Pupae in the subfamily Notodontinae show a great deal of morphological variation. One potential synapomorphy involves the shape of the terminal abdominal segments (A8–A10), which are broadly rounded (Figs. 7, 8) rather than being tapered as in other Notodontidae. Many notodontines have lost the cremaster, and these exhibit the rounded abdomen. However, the trait also occurs in taxa, such as *Notodonta*, where the cremaster is present (Ferguson, 1963).

Male and female pupae exhibit different external morphologies on the venter of the terminal segments, allowing one to distinguish the sexes (Jackson, 1890; Poulton, 1891; Mosher, 1918b). However, I did not examine this character complex from a taxonomic standpoint because often, specimens of only a single sex were available for study.

*Anterior margin of A10.* (18) In *Datana* and *Phalera* pupae, the anterior margin of A10 on the dorsal side bears a deep furrow (Poulton, 1891; Nagano, 1916; Mosher, 1918b; Dolinskaya, 1989). The posterior edge of this furrow is often sculpted (Fig. 26). Judging from the species I examined and figures in the literature, there is interspecific variation in shape. *Datana* species are extremely difficult to separate based on adult characters, so it would be interesting to see whether differences in furrow shape provide valuable species-specific characters.

There is an analogous modification in pupae of *Crinodes besckei*, where instead of a deep furrow, the anterior margin of A10 is sharply elevated and lip-shaped. This character does not occur in the other dudusine I examined, *Goacampa variabilis* (Figs. 9C, 23).

*Reticulate area on A10.* (19) Some pupae have a sharply raised, reticulate area on the dorsal surface of segment A10 just anterior to the cremaster. This structure was



Figs. 27–32. Scanning electron micrographs of notodontid pupae. 27. Cremaster and A10 of *Heterocampa guttivitta* Walker, dorsal view (200  $\mu\text{m}$ ). 28. Cremaster and A10 of *Symmerista leucitys* Franclemont, ventral view (200  $\mu\text{m}$ ). 29. Cremaster and A10 of *Ellida caniplaga* Walker, ventral view (200  $\mu\text{m}$ ). 30. Cremaster of *Zunacetha annulata* Guérin, ventral view (100  $\mu\text{m}$ ). 31. Cremaster of *Josia ligula* Hübner, ventral view (100  $\mu\text{m}$ ). 32. Cremaster setae of *J. ligula*, ventral view (50  $\mu\text{m}$ ). Scale lengths in parentheses.

discussed for two Palearctic species, *Fentonia ocypete* Bremer and *Spatalia argentina*, by Dolinskaya (1989). It also occurs in *Hyparpax perophoroides* (Strecker) (Ferguson, 1963) and *Misogada unicolor*. All these taxa belong in the subfamily Heterocampinae (Forbes, 1948; Miller, 1991). In *Heterocampa guttivitta*, this reticulate area consists of a few laterally oriented ridges (Fig. 27). In some heterocampines it is absent altogether. *Platychasma* has numerous, small longitudinal ridges on segments 9 and 10 (Fig. 5C), but these are probably not homologous with the structure in Heterocampinae.

*Cremaster shape.* (20) There is almost endless variation in cremaster morphology among Notodontidae; my study does not begin to tap the structure's taxonomic potential. Proper treatment of this character complex would require a monograph in itself. My goal here is to describe some of the variation, and to begin outlining ways in which the various character states might be useful for phylogenetic purposes.

In species belonging to at least six subfamilies—the Thaumetopoeinae, Notodontinae, Phalerinae, Dudusinae, Heterocampinae, and Nystaleinae—the cremaster is bifurcate (e.g., Figs. 3, 27, 28). There may be examples in other subfamilies as well. I apply a broad definition to this term, scoring any cremaster as bifurcate whose parts are divergent. A bifurcate cremaster may be the ground-plan state for the entire Notodontidae. The distinctive fork-shaped cremaster of Heterocampine (Figs. 10, 27) has been noted by various authors (Packard, 1895; Mosher, 1918b; Marumo, 1920; Ferguson, 1963), and it seems to be a definitive subfamily trait, at least for Holarctic species. A bifid cremaster with spiny projections (Fig. 26) is characteristic of *Datana* and *Phalera* (Dyar, 1891; Poulton, 1891; Mosher, 1918b).

Other cremaster types include the long, spine-like cremaster of *Closteria* (Packard, 1895; Nagano, 1916; Mosher, 1918b) and *Ellida* (Fig. 29), and the broad, compressed cremaster of Dioptinae (Figs. 30, 31).

Finally, there are notodontid pupae where the cremaster is entirely absent. This was described over a hundred years ago by Poulton (1891) and Dyar (1891) for species of *Cerura* and *Furcula* (Notodontinae), and has subsequently been discussed by other workers (e.g., Packard, 1895; Dolinskaya, 1989). In these species, the ninth and tenth abdominal segments are broadly rounded and the abdomen is completely smooth posteriorly (Fig. 7). An almost identical condition occurs in the genus *Gluphisia* (Packard, 1895; Ferguson, 1963; Dolinskaya, 1989; Fig. 8). I previously made the suggestion (based on larvae and adults) that *Cerura/Furcula* and *Gluphisia* not only belong together in the same subfamily, the Notodontinae, but that they belong in the same tribe, the Dicranurini (see Table 1). Cremaster morphology provides another synapomorphy in support of my hypothesis.

*Base of cremaster fluted.* (21) The base of the cremaster in all dioptine pupae I examined has a characteristic series of longitudinal ridges on its ventral surface. A possibly homologous condition occurs in Nystaleinae, where the cremaster is a different shape than in Dioptinae but also has longitudinal ridges at its base. Adult and larval data show that these two subfamilies are sister groups (Weller, 1989; Miller, 1991), and I draw attention to this character as another potential synapomorphy.

*Cremaster setae.* (22) In many families of Lepidoptera there are hook-shaped setae on the cremaster (Fig. 32). These setae can serve either to anchor the pupa to the lining of the cocoon, or in species lacking a cocoon, to attach it to a silk pad on the substrate spun previously by the caterpillar (Common, 1990). There are four pairs of cremaster setae in most Geometridae, and a nomenclature ("D1, D2, L1, SD1")

has been applied to them (e.g., see Bolte, 1990). Presumably, these terms were derived from the primary setal names on the anal plate of larvae (McGuffin, 1987). Although eight is also a typical number of cremaster setae for Notodontidae (see below), I could not homologize those in notodontids with the ones in Geometridae, and so have not applied setal names.

Mosher claimed that presence of hooked setae "is the exception in the Notodontidae, as most of them pupate in the ground" (1916b:58), implying that pupation in the ground obviates the need for setae. I found that hook-shaped cremaster setae occur in six of the nine notodontid subfamilies. Based on my survey, the groups in which they are absent are the Thaumetopoeinae (Fig. 3), Phalerinae (Fig. 26), and Heterocampinae (Fig. 27). Mosher (1918b) used this as diagnostic for Heterocampinae. Among members of the subfamily Notodontinae, setae occur in *Notodonta* (Ferguson, 1963) and other more primitive members of the group, but they are obviously absent in taxa that lack the cremaster altogether (see above).

Where setae do occur, they vary in number from only eight in *Symmerista* and *Notodonta* (Ferguson, 1963) to over 20 in *Platychasma* (Fig. 5). The outgroup number is about 20 as well (*Doa ampla*, Fig. 2). There is also variation within subfamilies. For example, among the Dioptinae numbers range from eight or ten setae in *Josia* and *Zunacetha* (Figs. 30–32) to about 25 in *Cyanotricha necyria*. *Phryganidia californica* (Dioptinae) is unique in having hook-shaped setae on the dorsum of segments A7–A9, as well as on the cremaster itself (Miller, 1987). The long cremaster of *Closterera* species (Pygaerinae) has a few stout terminal hooks, each bearing tiny setae that Mosher (1918b) noted are easily destroyed and difficult to see.

#### Body shape:

*Body dorso-ventrally compressed.* (23) Both Dyar (1891) and Packard (1895) noted that the body of *Cerura* pupae is slightly flattened dorso-ventrally. Packard (1895) also applied that description to the pupae of *Gluphisia* species. He did not, however, use the character as evidence of relationship between the two genera. Although not particularly well-marked in *F. scolopendrina* (Fig. 7B), the trait is readily apparent in other *Furcula* species (Dyar, 1891) as well as in *Cerura*, and it can easily be seen in *Gluphisia septentrionis* (Fig. 8B).

*Body wide relative to its length.* (24) There is considerable variation in body proportion among the species I studied. I recognized two character states for this trait: in the majority of taxa the body is elongate, while in three taxa—*Thaumetopoea*, *Furcula* and *Gluphisia* (Figs. 3, 7, 8)—the body is wide relative to its length.

#### CLADISTICS OF PUPAL DATA

Analysis of the data matrix in Table 3, with all nine multistate characters except proboscis length and antenna length (Characters 3 and 5) treated as non-additive, produced a single tree (Fig. 33). There are several important features of that cladogram. First, taxa that I claimed are related based on adult and larval morphology (Miller, 1991) also group together when pupal characters are used. This is a significant result; some of my previous conclusions—such as placement of *Gluphisia* with *Furcula*, and *Crinodes* with *Goacampa*—might be considered controversial.

Second, the subfamily tree based on pupae (Fig. 34) corresponds well with previous hypotheses. For example, two pupal synapomorphies (Characters 16 and 21) unite

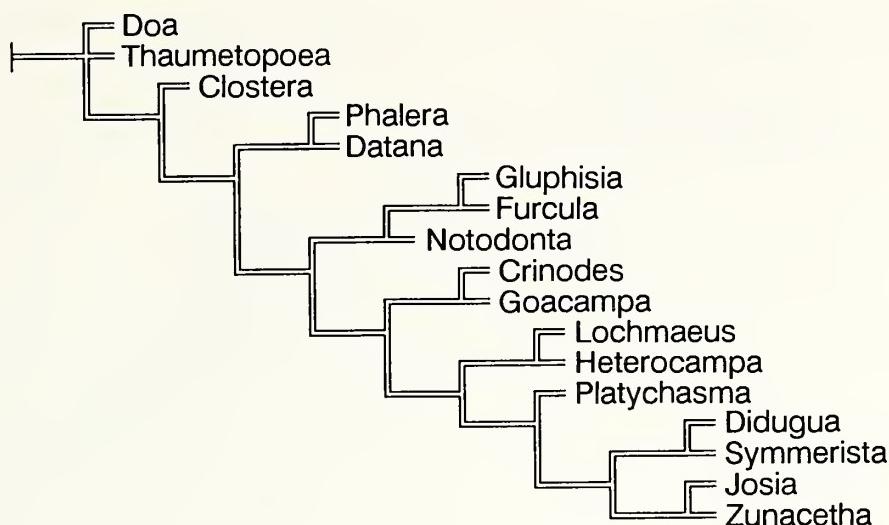


Fig. 33. Cladogram produced by a Hennig86 analysis of 24 pupal characters for 16 species of Notodontidae (see Tables 1, 2) with *Doa ampla* as an outgroup. Length = 52, CI = 71, RI = 80.

the Dioptinae and Nystaleinae, a theory supported by adult and larval data (Weller, 1989; Miller, 1991). Comparison of my adult/larval tree (Fig. 1) with the one from pupae in fact shows only two differences: In the pupal cladogram (Fig. 34), the Phalerinae appear two nodes lower than before, while the subfamily Platychasmatinae has moved higher, appearing as the sister group to the Dioptinae + Nystaleinae.

To further test these comparisons, I combined the 174 characters from my adult/larval matrix (Miller, 1991: appendix IV) for the 17 test species with the 24 pupal characters (Table 3). This produced a single data matrix, containing 198 characters, derived from all three life stages. Analysis of that matrix using Hennig86 and implicit enumeration again gave a single tree (Fig. 35). According to this cladogram, the position of the Phalerinae suggested by pupal morphology (Fig. 34) may be the correct one. On the other hand, the combined analysis supports placement of the Platychasmatinae as suggested by adult and larval characters (Fig. 1); rather than being a

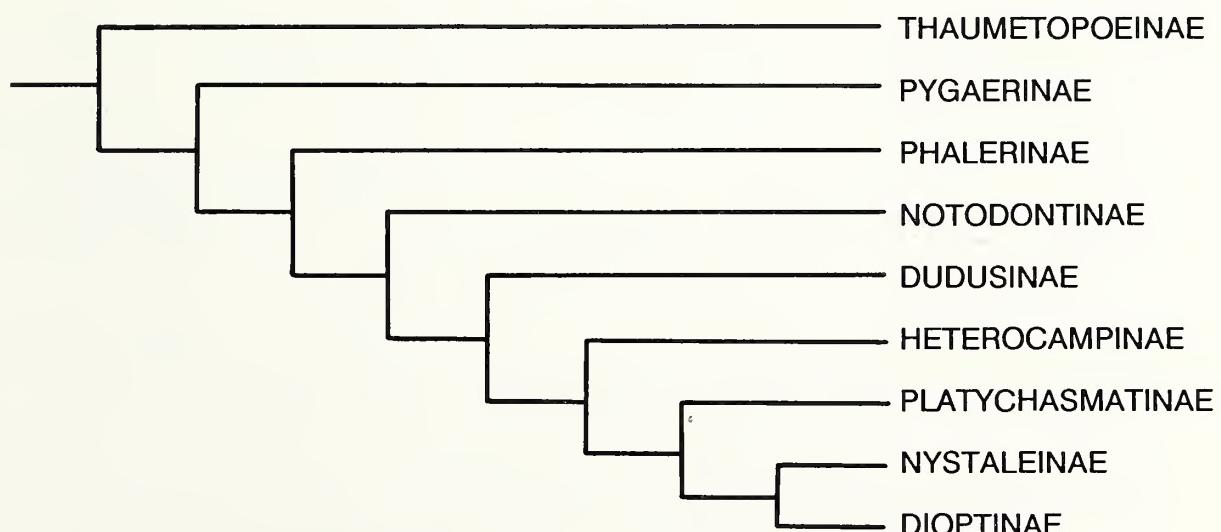


Fig. 34. Relationships among notodontid subfamilies as implied by the cladogram in Figure 33.

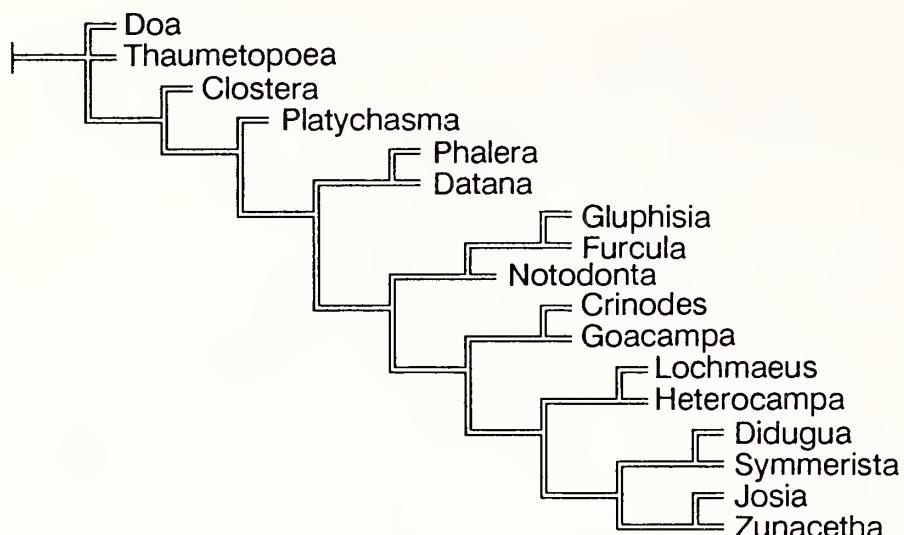


Fig. 35. Cladogram produced by a combined matrix of adult, larval, and pupal characters (total = 198; see text) for 16 species of Notodontidae with *Doa ampla* as an outgroup. Length = 367, CI = 62, RI = 62.

derived group, the Platychasmatinae is the sister-group of all notodontid subfamilies exclusive of the Thaumetopoeinae and Pygaerinae.

Perhaps the most important result of my research on pupal morphology is the discovery of potential synapomorphies for notodontid subfamilies, summarized in Table 4. Clearly, all of my conclusions will be subject to change as pupae from additional notodontid taxa are studied and as more is learned concerning morphology of this life stage.

#### KEY TO THE PUPAE OF NOTODONTID SUBFAMILIES

Mosher (1918b: 58–60) gives a key to pupae for six North American notodontid genera representing five subfamilies. The key below treats all nine of the currently recognized subfamilies (see Miller, 1991). However, the user should be reminded that it is based on relatively few taxa. In particular, pupae of Neotropical and Old World species may not key out successfully.

1. Proximo-lateral angles of proboscis extending to eye-pieces (Figs. 5, 6, 8–12) .... 4
- Proximo-lateral angles of proboscis not extending to eye-pieces (Figs. 3, 4, 7) .... 2
- 2(1). Cremaster present; eye-piece not small ..... 3
- Cremaster absent; eye-piece small ..... *Furcula*, *Cerura* (Notodontinae; Fig. 7)
- 3(2). Labial palpi absent; abdominal cuticle covered with fine wrinkles; abdominal spiracles small; body wide; cremaster composed of two horns .. *Thaumetopoeinae* (Fig. 3)
- Labial palpi present; abdominal cuticle covered with small pits; abdominal spiracles large; body elongate; cremaster a single elongate spine with hooks at tip ..... Pygaerinae (Fig. 4)
- 4(1). Anterior suture of proboscis not strongly curved, arching only slightly forward at midline, proximo-medial angles of proboscis not acute (Figs. 5–8) ..... 5
- Anterior suture of proboscis strongly curved, arching sharply forward at midline, proximo-medial angles of proboscis acute (Figs. 9–12) ..... 7
- 5(4). Antennae extending beyond mesothoracic legs; proboscis as long as wings; forewing venation quadrifid; cremaster with more than 20 hook-shaped setae ..... Platychasmatinae (Fig. 5)

Table 4. Summary of potential subfamily synapomorphies from pupal morphology. Characters are based on study of the species listed in Table 1.

- Thaumetopoeinae*: (1) Labial palpus sclerite absent; (2) cremaster setae absent; (3) body wide relative to its length.
- Pygaerinae*: (1) Cremaster long and spine-shaped, with stout hooks at tip.
- Platychasmatinae*: (1) Forewing venation quadrifid; (2) Antennae extending beyond mesothoracic legs; (2) Dorsum of A10 with numerous, fine longitudinal ridges.
- Notodontinae*: (1) Terminal segments of abdomen broadly rounded.
- Phalerinae*: (1) Abdomen covered with large, deep pits; (2) Antero-dorsal margin of A10 with a deep furrow; (3) Cremaster setae absent.
- Dudusinae*: (1) Dorsum of thorax with a distinct crest along midline; (2) Caudal margin of mesothorax with a series of shallow depressions separated by longitudinal striations; (3) Anterior margin of each movable segment with a distinct carina.
- Heterocampinae*: (1) Caudal margin of mesothorax with a series of small, quadrangular plates separated by deep pits; (2) Anterior margin of each movable abdominal segment ringed with a diffuse band of small pits; (3) Dorsum of A10 with a reticulate area anterior to cremaster; (4) Cremaster fork-shaped, lacking setae.
- Nystaleinae*: (1) Labial palpus sclerite present; (2) Thoracic cuticle covered with deep pits; (3) Anterior margin of each movable abdominal segment ringed by a single row of lunate pits.
- Dioptinae*: (1) Thorax long, equal to  $\frac{2}{3}$  total body length; (2) Caudal margin of mesothorax projecting posteriad at body midline; (3) Antennae extremely long, often touching A5; (4) Abdominal spiracles small; (5) Cremaster broad, compressed.

- Antennae not extending beyond mesothoracic legs; proboscis shorter than wings; forewing venation trifid; cremaster with fewer than 10 setae or with setae absent (Figs. 6-12) ..... 6
- 6(5). Terminal abdominal segments (A8-A10) broadly rounded; abdomen covered with small pits; dorsum of A10 unmodified; cremaster often reduced or absent, but when present setae occur ..... *Notodonta, Gluphisia* (Notodontinae; Fig. 8)
- Terminal abdominal segments tapered; abdomen covered with large, deep pits; dorsum of A10 with a deep furrow; cremaster a series of spines, setae absent ..... Phalerinae (Figs. 6, 26)
- 7(4). Caudal margin of mesothorax strongly sculpted; abdominal spiracles facing laterally; base of cremaster lacking flutes on ventral surface; labial palpi absent (Figs. 9, 10) ..... 8
- Caudal margin of mesothorax not strongly sculpted; abdominal spiracles facing posteriorly; base of cremaster with longitudinal flutes on ventral surface; labial palpi often present (Figs. 11, 12) ..... 9
- 8(7). Caudal margin of mesothorax with a series of shallow depressions separated by raised ridges; thorax with a dorsal crest along midline; anterior margin of each movable abdominal segment (A5-A7) with a carina ..... Dudusinae (Figs. 9, 14, 23)
- Caudal margin of mesothorax with a series of small, quadrangular plates separated by deep pits; thorax without a dorsal crest; anterior margin of each movable abdominal segment with a diffuse band of small pits, no carina ..... Heterocampinae (Figs. 10, 15-18, 21, 27)
- 9(7). Surface of thorax deeply pitted; thorax not elongate; mesothorax unmodified; anterior margin of each movable segment with a single row of lunate pits; proboscis only as long as wings; cremaster bifid, not dorso-ventrally compressed ..... Nystaleinae (Figs. 11, 19, 22, 28)

- Surface of thorax with a few small pits or smooth; thorax elongate,  $\frac{2}{3}$  the length of abdomen (ventral view); anterior margins of movable segments unmodified; proboscis often longer than wings, touching A5; cremaster dorso-ventrally compressed, not bifid ..... Dioptinae (Figs. 12, 30–32)

#### DISCUSSION

According to Mosher, “the pupae of [Notodontidae] vary considerably, and there is no one character which will serve to separate them from those of the nearly related families” (1918b:58). None of the diagnostic characters she listed for the Notodontidae (Mosher, 1916b, 1918b) adequately define the group; most are plesiomorphic traits. Both Mosher and Common (1990) emphasized reduction or loss of labial palpi as definitive (see Character 2). Unfortunately, this character is extremely variable among families of Lepidoptera. For example, within the Noctuoidea labial palpi are present in Noctuidae but absent in Arctiidae (Mosher, 1916b). Minet (1991) used reduction of labial palpi in pupae to define a large ditrysian clade that includes the Geometroidea, Hedyloidea, Hesperioidea, and Papilionoidea.

Another pupal trait that Mosher (1916b, 1918b) and Common (1990) stressed in their family diagnoses is presence of punctures on the abdomen. I found, however, that these punctures are absent in *Thaumetopoea pinivora* (representing the subfamily Thaumetopoeinae; see Character 14), so the trait cannot be used to define the Notodontidae. None of the other characters listed by either Mosher or Common can be used as potential family-level synapomorphies.

My own study does little to alleviate this problem; I was unable to find a pupal character unique to the Notodontidae. I can only recommend that future researchers pay attention to morphological detail in the search for a synapomorphy in pupae. If one is to be found, it will not likely involve an obvious feature of the external anatomy. However, lack of a synapomorphy from pupae does not call monophyly of the group into question; there are numerous synapomorphies from adults and larvae (Miller, 1991).

Notwithstanding the problems outlined above, research on pupae makes clear the potential of this life stage for understanding the phylogeny and systematics of the Notodontidae. I have identified pupal traits that elucidate relationships among subfamilies (e.g., Characters 1, 3, 4), as well as traits that help define subfamilies (Table 4). Future research should focus on the pupae of notodontid groups, such as the Hemiceratini, whose positions in the family classification remain enigmatic (see Miller, 1991). Perhaps characters from pupae will provide answers that have not been forthcoming from the study of adults and larvae.

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**FRANCLEMENTIA INTERROGANS (WALKER), A  
NEW GENUS FOR AN OLD SPECIES  
(LEPIDOPTERA: NOCTUIDAE: AMPHIPYRINAE)**

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*Abstract.*—The identity of *Leucania interrogans* Walker, 1856, described from an unknown type locality, is confirmed, and a lectotype is designated for it. It is a distinctive and rarely collected species of amphipyrine noctuid of the southeastern U.S. that belongs to neither *Leucania* nor *Phragmatiphila*, where placed by previous authors. A comprehensive search failed to reveal any genus to which *interrogans* might be referred, and *Franclemontia*, new genus, is proposed for it. The possible sister-group relationship of this new genus to atypical North American elements of *Chortodes* is suggested. All members of this large group of amphipyrine genera are believed to be host-specific stem borers in marsh grasses.

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Walker (1856:114) described *Leucania interrogans* from two specimens from the Milne collection in the British Museum but gave no type locality. Hampson (1910: 270) transferred *interrogans* to his newly described genus *Phragmatiphila* and provided an illustration of one of the syntypes, but their country of origin remained unknown for about a century. John G. Franclemont, while stationed at Fort Rucker, Ozark, Dale Co., Alabama, in the early 1940's, collected a specimen that he subsequently recognized as *P. interrogans*. After Hampson, however, no mention of the name is also in the 1983 check list (Franclemont and Todd, *in* Hodges et al., 1983). The Milne collection is known to have contained material purchased from John Abbot (Doubleday [1839], *in* Scudder, 1869:123), and Abbot was about the only source of moths from the southeastern United States prior to Doubleday's stay at St. Johns Bluff, Duval County, Florida, in 1838. Georgia is therefore the probable type locality.

Few have been collected, probably no more than eight or ten specimens, including the two types in the Natural History Museum, London (BMNH). A male and female (Figs. 3, 4) from The Wedge Plantation, McClellanville, Charleston County, South Carolina, are deposited in the National Museum of Natural History (USNM). Others include the specimen collected by Franclemont at Fort Rucker, Alabama and another from McClellanville, South Carolina (Cornell Univ. Coll.); and one from near Pensacola, Escambia County, Florida that was reported by Kimball (1965:103) from the Shirley M. Hills collection, and probably identified for Kimball by Franclemont. The present location of the Hills collection could not be determined. I have been advised of two other specimens in private collections but have not seen them. The species remained in the genus *Phragmatiphila* from 1910 to the present, although it bears little resemblance to the type species of that genus, the European *Phragmatiphila nexa* (Hübner) (Figs. 5–7, 12).

*Phragmatiphila nexa* appears to be more closely related to species of the North American genus *Meropleon* Dyar, which I revised earlier (1982). Although the male

genitalia of the two genera agree closely, the female genitalia differ enough to dissuade me from synonymizing them. Also, *P. nexa* has a conspicuous, s-shaped, white discal spot on the forewing not present in any species of *Meropleon*. A similarly shaped but less conspicuous s-shaped discal spot is present in *P. interrogans*, however, and this may be why Hampson associated the species with *Phragmatiphila*.

A review of similar moths worldwide, including other species of *Phragmatiphila* as now understood (Poole, 1989, vol. 2:800) failed to reveal anything that could be considered congeneric with *interrogans*. In the event that such a species exists, it would need a generic name. I establish the following genus to accommodate this rare and little-known species.

### Franclemontia, new genus

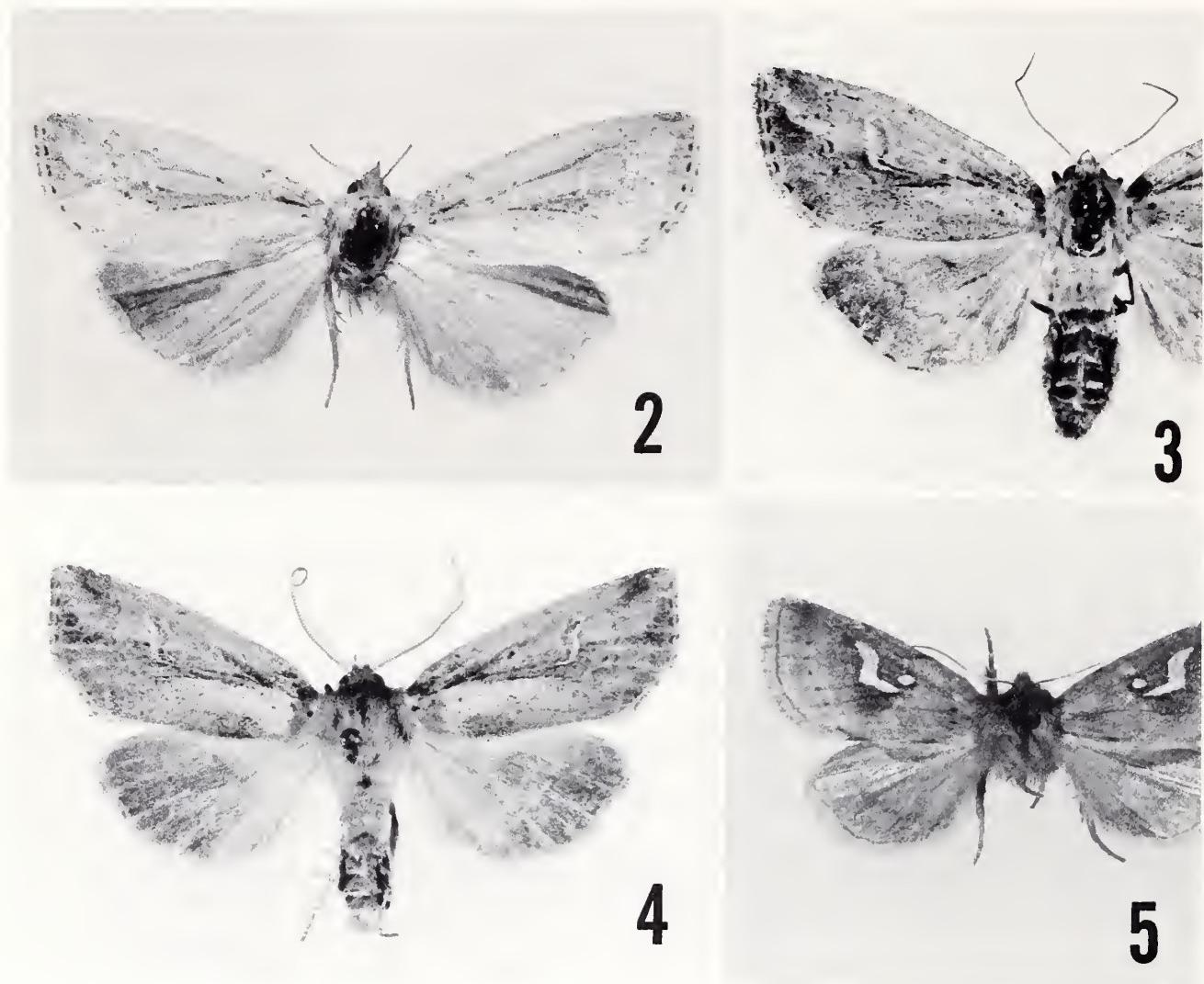
Type species: *Leucania interrogans* Walker, 1856. Monotypic.

The features that distinguish this genus are summarized in the accompanying list (Fig. 1), and the following notes will explain them:

1. *Franclemontia interrogans* (Figs. 2–4, 8–11) is unique among the genera to which it seems most closely related in having wide, bipectinate male antennae. Although I mentioned (1982:231) that *Meropleon titan* has bipectinate male antennae with short branches, they are really more lamellate than pectinate. *Franclemontia* has true bipectinate male antennae with branches whose length may equal nearly 4 times the thickness of the antennal shaft.
2. Neither *F. interrogans* nor species of *Meropleon*, or any other species examined, have the sharp, bladelike, transverse frontal process that distinguishes *P. nexa*, and which is visible even without removing the frontal vestiture. Species of most genera have a somewhat convex, rounded front, although the “*Chortodes*” species that I listed as Group B have an obtusely conical front with a decumbent, pointed apex.
3. *Phragmatiphila nexa* (Fig. 5) has a conspicuous, s-shaped or z-shaped reniform spot somewhat similar in shape to the less distinct reniform of *F. interrogans*.
4. The male of *interrogans* has a pair of eversible scent glands with coremata or long hair pencils, each contained in a lateral pocket at the base of the abdomen (Fig. 10). These recessed bundles of hair extend for the length of the first three abdominal segments. No similar structures were found to be present in any of the related grass-feeding amphydine genera investigated, although they appear elsewhere in the Amphydinae.
5. The uncus is flattened and widest in the middle, tapering both toward the apex and base. *Phragmatiphila nexa* is the only other species examined that has this type of uncus. That of the Australian *Bathytricha truncata* Turner is also wide but not tapered.
6. The anellus is thick and leathery and finely and densely scobinate over much of its surface in *Phragmatiphila* and *Meropleon*, but not so in *Franclemontia*, *Chortodes*, or other genera studied except *Bathytricha* from Australia.
7. The juxta is deeply notched or v-shaped in *Franclemontia* and *Phragmatiphila* but not in other genera. “*Chortodes*” Group B is unusual in having the juxta shaped like a spear point or arrowhead.

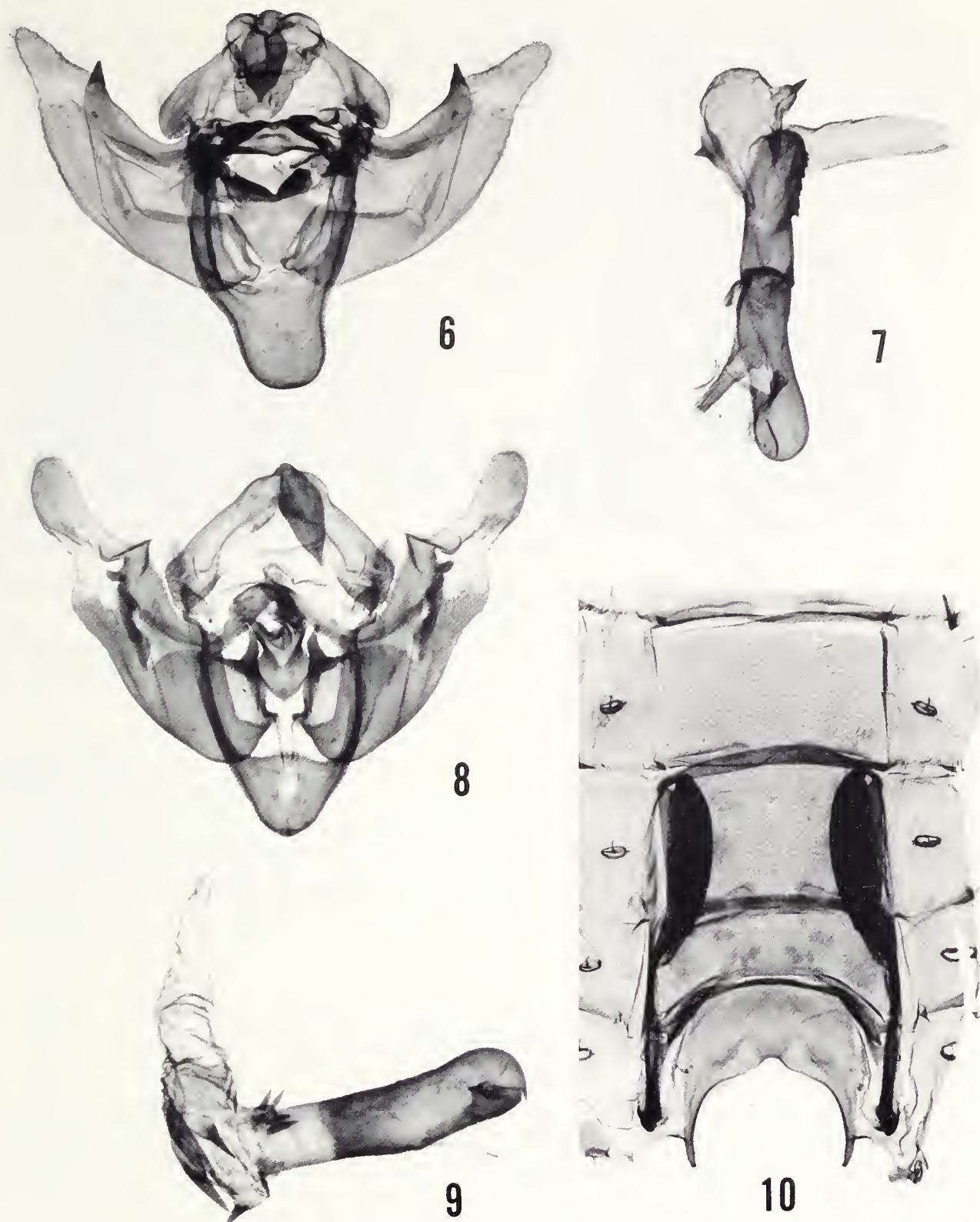
		<u>Francl.</u>	<u>Phrag.</u>	<u>Meropleon</u>	Chortodes Group A	Chortodes Group B
1	Bipectinate ♂ antenna	+	-	-	-	-
2	Frontal process absent	+	-	+	+	-
3	S-shaped reniform	+	+	-	-	-
4	Hair pencils at base of ♂ abdomen	+	-	-	-	-
5	Uncus broad in middle	+	+	-	-	-
6	Anellus not leathery or scobinate	+	-	-	+	+
7	Juxta notched or V-shaped	+	+	-	-	-
8	Cucullus developed (may be rudimentary)	+	-	-	+	+
9	Ampulla	+	+	-	+	+
10	Digitus	+	-	-	-	±
11	Large costal sclerite and costal process	+	+	+	-	±
12	Sacculus swollen, with large costal lobe	+	-	-	-	+
13	Clavus a long, pointed process	+	-	-	-	-
14	Aedoeagus with ventro- distal serrate ridge	+	+	-	-	+
15	♀ genitalia short, stout	+	-	-	-	±
16	Ovipositor lobes straight, pointed	+	-	-	-	-

Fig. 1. Selected characters of *Franclemontia* and related genera. Plus and minus signs indicate presence or absence. *Francl.* = *Franclemontia*; *Phrag.* = *Phragmatiphila* (others spelled out).



Figs. 2–5. Adult moths. 2. *Franclemontia interrogans* (Wlk.) ♀. Lectotype (BMNH). 3. *F. interrogans* ♀. Wedge Plantation, McClellanville, S.C., 29 April 1973, R. B. Dominick (USNM). 4. *F. interrogans* ♂, same locality, 7 April 1977, D. C. Ferguson (USNM). 5. *Phragmatiphila nexa* ♂. Germany (USNM). Magnification: 2×.

8. The valve of the male genitalia of *Franclemontia* has a fairly well-formed cucullus, although no coronal spines are present. However, every stage from no cucullus to a fully developed triangular one may elsewhere be found within one genus (e.g., *Chortodes*).
9. A small ampulla is present in *F. interrogans* and *P. nexa*, although that of *nexa* is minute.
10. A digitus, or digitus-like process, occurs in *Franclemontia*, although elsewhere in this immediate group a possible homologue may be seen only in one of the two species of "Chortodes" Group B ("C." *enervata* (Guenée)).
11. The large, bowed, concave, costal sclerite of the valve, which is an especially conspicuous feature of all species of *Meropleon*, is similar in *P. nexa*. It is present in modified form in *F. interrogans* and *Chortodes enervata*. The costal sclerite, when present, has a pointed or scoop-shaped free end  $\frac{1}{2}$  to  $\frac{2}{3}$  of the way out the costa. In *F. interrogans* this free process is about halfway out and takes the form of a triangular costal process of unique form, as may be seen



Figs. 6–10. Male genitalia. 6. *Phragmatiphila nexa* (Germany). 7. Same specimen, aedeagus. 8. *Franclemontia interrogans*, genitalia of specimen shown in Figure 4. 9. Same specimen, aedeagus. 10. Same specimen, abdominal sterna 1–4, showing evversible structures with hair pencils (Character 4).

- in Figure 8. The j-shaped binary sclerite at this site in "*C.*" *enervata* is probably derived from a fusion of the pointed costal sclerite and an enlarged digitus.
12. In *Franclemontia* the sacculus is swollen and rounded, forming a costal lobe almost reaching the costobasal angle of the valve. The sacculus of "*Chortodes*" *enervata* is similar, but without the clavus.
  13. *Franclemontia interrogans* is unusual in having a clavus in the form of a long, sharp, thornlike process arising from the costal lobe of the sacculus. These processes lie in the same plane as the juxta and flank it, one on each side. No other American members of the group have a clavus.
  14. The aedeagus of *Franclemontia* has 3 large, acute, dentate processes (cornuti) on the vesica, and 5 smaller ones on the distal end of the aedeagus, clustered in two groups subventrally. Although I equated those on the aedeagus with the similarly situated, longitudinally serrate ridge of *Phragmatiphila nexa*, it is doubtful whether the two structures are homologous. Those of *Franclemontia* suggest *Meropleon* and the arrangement in *P. nexa* is found otherwise only in the species of "*Chortodes*" Group B.
  15. The female genitalia are unusually shortened longitudinally, from ovipositor to and including the corpus bursae, and have a short, thick, rugose "neck" on the bursa copulatrix. The female genitalia of "*Chortodes*" *defecta* are surprisingly similar in almost every detail.
  16. The ovipositor lobes of the female genitalia are straight and pointed, not blunt and bent somewhat ventrad as in most other genera of the group. In *P. nexa* they are rounded at the tips but not downcurved.

The genus *Chortodes* Tutt is a holarctic group treated in North American check lists as *Hypocoena* Hampson, but recently regarded as a senior synonym of *Hypocoena* (Kononenko, Lafontaine and Mikkola, 1989). However, the American species include at least two genera, which explains why I list them as Groups A, *Chortodes sensu stricto*, and B, "*Chortodes*." Group B includes *C. enervata* (Guenée) and *C. defecta* of authors (not Grote). Group A consists of all others, including the type species, *C. morrisii* Dale.

*Franclemontia interrogans* (Walker), New Combination  
Figs. 2–4, 8–10

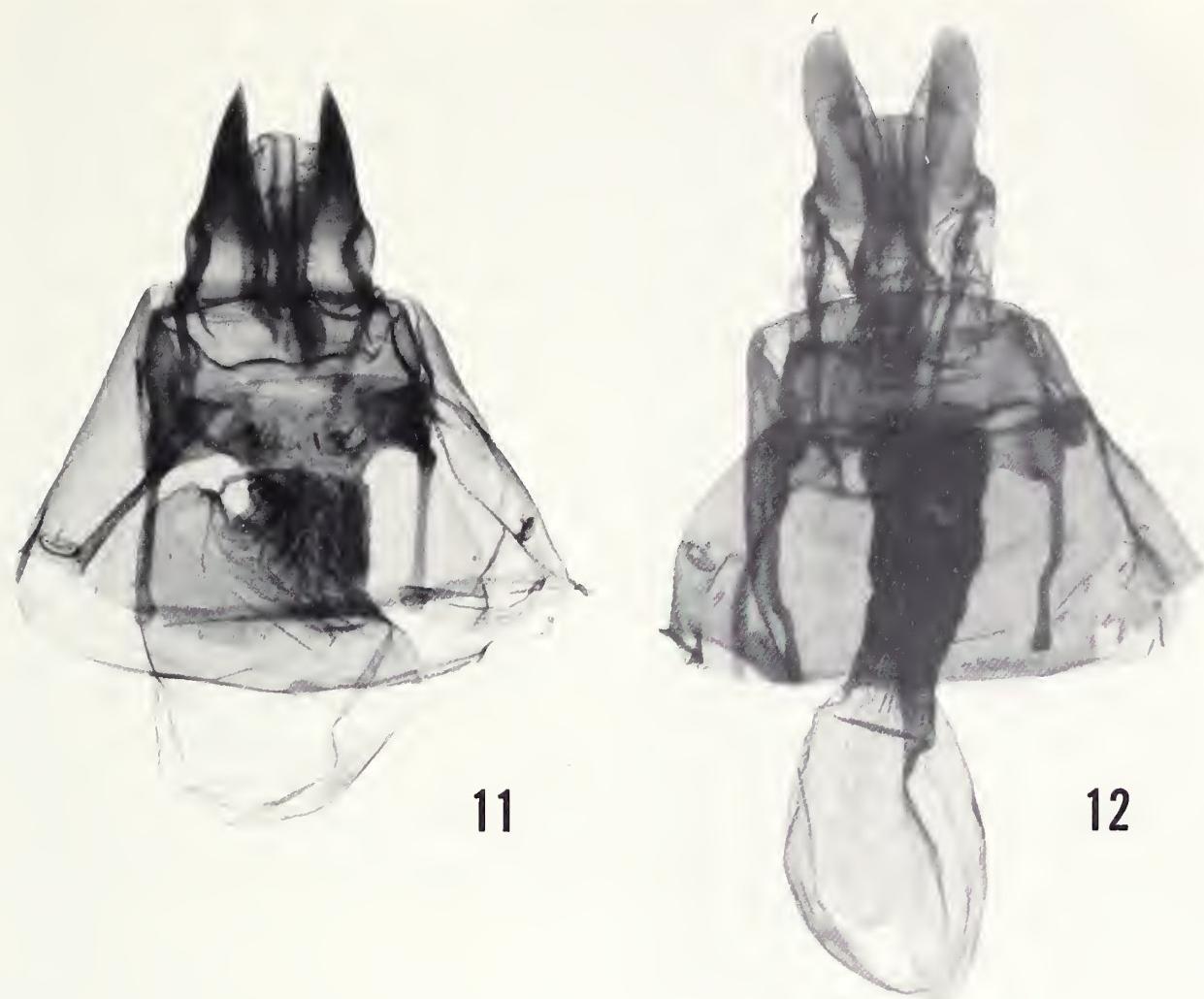
*Leucania interrogans* Walker, 1856:114.

*Phragmatiphila interrogans* Hampson, 1910:270, pl. 143, fig. 3; Kimball, 1965:103; Franclemont and Todd, *in* Hodges et al., 1983:138.

**Type locality:** Not given [probably Georgia—see earlier comment].

**Types:** Described from a male and female, of which the female was illustrated by Hampson (1910, pl. 143, fig. 3) and is figured again in this paper (Fig. 1). I hereby designate this female syntype as the lectotype. The male syntype cannot now be found, although its genitalia are preserved in a vial in the collection of The Natural History Museum, London.

**Description:** Although the generic description serves also to characterize the species, inasmuch as there is only one, I offer the following supplementary information to eliminate any doubt that might remain concerning the identity of the species. Male



Figs. 11, 12. Female genitalia. 11. *Franclemontia interrogans*, genitalia of specimen shown in Figure 3. 12. *Phragmatiphila nexa* (Sweden).

antenna with longest pectinations equal to more than 3 times diameter of antennal shaft; female antenna simple. Eyes large, very slightly elliptical, protuberant, equal to full hemisphere in female, slightly more than hemisphere in male. Palpi long, porrect or somewhat upturned; second segment as long as eye, third segment  $\frac{1}{3}$  as long as second in both sexes (palpal vestiture mostly worn off in specimens examined). Frons rounded and bulging, but not conical or ridged. Proboscis only slightly reduced, about as well developed as those of *Chortodes* species (described as rudimentary in potentially related African genera). Legs long and normally developed, with long hindtibial spurs, the longest being slightly longer than the second palpal segment; hind leg slightly shorter and with tibia more swollen in female; legs roughly and loosely scaled, with thin posterior fringe of longer, hairlike scales; epiphysis reaching almost to end of foretibia. Vestiture of vertex and thorax consisting of long hairlike scales, but with some broad scales concealed beneath; thorax and abdomen without special scale tufts or crests.

Hindwing with vein  $M_2$  obsolescent. Shape of male and female forewings differ; that of male normal except that outer margin is noticeably angled at vein  $M_3$ ; female forewing not angulate on outer margin but with costa unusually convex or arched.

Forewings pale brown, the usual dead-grass color of many grass-feeding moths, with slightly darker, predominantly longitudinal shades, and the following markings: a pale, somewhat indefinitely s-shaped or z-shaped reniform with an elongated dark center, bending distad in direction of outer margin at end near costa and basad at end nearest inner margin; the latter end tapering off very acutely as a thin, pale-edged, dark streak directed toward wing base; a dark-brown dot, ringed by a paler shade, at position of orbicular; a small, black, basal dot; and a weak, sinuous, dark, postmedial line broken into a series of dots or dashes (antemedial line obsolete). Hindwing almost unicolorous gray brown in male; slightly paler, more variegated, and with a distinct, dusky, sinuous, transverse band in female. Undersurfaces with forewing darker than hindwing but with contrastingly paler costa and outer margin, at least in female; diffuse, dusky, discal spots on both wings, that on hindwing of female preceded by a thin, short, longitudinal dark streak; hindwing also with weak, dark, convex postmedial line, especially apparent in female. Terminal line a broken series of dark crescents or dashes on both upper- and undersurfaces of both wings. Length of forewing: ♂, 15 mm (N = 1); ♀, 15–16 mm (N = 2).

**Genitalia.** Discussed under genus and illustrated. The male (Figs. 8, 9) is unusual in many respects, including the possession of what appears to be a small digitus, a structure normally absent in members of this group. The digitus in this case, however, may be an ampulla that has migrated to a different position. The female genitalia (Fig. 11), with their short, stout overall aspect and wide, straight, rigid, rugose neck region of the bursa copulatrix, would be unique were they not almost identical to the female genitalia of "*Chortodes*" *defecta* (Grote), previously known as *Hypocoena* *defecta* (Grote).

**Distribution.** SOUTH CAROLINA: Wedge Plantation, near McClellanville, Charleston Co. FLORIDA: near Sarasota, Escambia Co. (Kimball, 1965). ALABAMA: Fort Rucker, near Ozark, Dale Co. (Franclemont Coll., Cornell Univ.). The types are probably from Georgia, but this is speculative.

**Flight period.** The only collection dates available are 7, 15 and 21 April for South Carolina; 6 April for Florida; and 5 April for Alabama. The species is undoubtedly univoltine, as are probably all grass-boring Amphipyrinae in North America.

**Habitat.** The South Carolina specimens were taken at light near old, abandoned, plantation rice fields (now brackish) at the edge of the vast Santee Delta marshes, on the south side of the South Santee River about 8 km (5 miles) upstream from the coast. I would therefore have guessed that the species is associated with some select microhabitat in salt or brackish estuarine marshland; the Florida site could have been similar. However, the locality in Alabama is not coastal.

#### DISCUSSION

Each of the genera herein used for comparison (Fig. 1) has other distinguishing features not mentioned. For example, *Phragmatiphila nexa* is the only member of the complex with a signum, which is small and depicted edgewise on the right side of the bursa in Figure 12. Species of *Meropleon* are consistent in having a unique fringe of persistent (hard-to-remove) scales on the posterior margin of the seventh sternum of the female abdomen. Males of both species of "*Chortodes*" Group B have a distinctive *juxta* that is shaped like an arrowhead or spear point.

I also examined genitalia, or published illustrations of genitalia, representing a wide array of other genera of amphydipine noctuids whose species bore in grass stems, indeed, all that could be identified as containing species that might be related to *F. interrogans*. Species of the following genera were included in this survey, in most cases the type species: *Archana* Walker, *Chortodes* Tutt (=*Hypocoena* Hampson), *Spartiniphaga* McDunnough, *Ommatostola* Grote, *Benaminiola* Strand, *Mammifrontia* Barnes and Lindsey (North America); *Nonagria* Ochsenheimer, *Photedes* Lederer, *Rhizedra* Warren (Europe); *Arapex* Hampson, *Busseola* Thurau, *Carelis* Bowden, *Conicofrontia* Hampson, *Poecopa* Bowden, *Poeonoma* Tams & Bowden, *Sciomesa* Tams & Bowden, *Sesamia* Guenée, *Speia* Tams & Bowden (Africa, Asia), and *Bathytricha* Turner (Australia).

I examined the genitalia of all species of *Meropleon* Dyar (Ferguson, 1982) and *Chortodes* in related revisionary projects. *Nonagria*, widespread in the Old World, is clearly more different. Many of the above-mentioned genera are African, and I had thought that the sister group of *Franclemontia* might be found among them. For example, *Conicofrontia* and *Sciomesa* show certain similarities to *Franclemontia* in valve shape, and *Sciomesa* has pectinate male antennae. However, *Franclemontia* does not fit any of those genera because of other important differences, such as the hair pencils at the base of the male abdomen, the long thornlike clavus, and the short, stout female genitalia. Keys and illustrations for the African genera were given by Janse (1939), Tams and Bowden (1953) and Bowden (1956). The Australian genus *Bathytricha*, of which I saw the male genitalia of a specimen believed to be *B. truncata* (Walker) (the type species), kindly sent by T. L. McCabe, is also related to this group. The valve (including character 11) is remarkably similar to that of *Phragmatiphila* and *Franclemontia*, although the sclerites it bears are more similar to those of *Chortodes enervata*. It has bipectinate male antennae (character 1), a broad uncus (character 5), a scobinate anellus (character 6), a rudimentary cucullus (character 8), and a cockscomb-shaped sclerite on the aedoeagus (character 14). However, characters 3, 4, 7, 9, 12, and 13 appear to be absent. In the end I concluded that the closest relatives of *Franclemontia* are also North American, and almost certainly the species of *Chortodes* Group B.

Curiously, this whole complex of genera appears to be unrepresented in the neotropics. For example, the only New World species of *Arapex*, an otherwise Old World tropical genus, is also found in the warm-temperate zone of eastern North America, not in the American tropics (Ferguson, 1991).

My inspiration for the generic name *Franclemontia* needs little explanation. I was one of Dr. Franclemont's earlier graduate students, and one whose career in Lepidoptera systematics might never have happened had our paths not crossed. It is an honor to me to be the one to name a genus after him, and I have tried to fit the name to an appropriate moth.

#### ACKNOWLEDGMENTS

I thank R. W. Poole, a colleague in the Systematic Entomology Laboratory, for answering queries concerning the world fauna and the possible relationships of *Franclemontia*; and Linda Pitkin and Martin Honey, the Natural History Museum, London, for sending on loan the type material of *Leucania interrogans* Walker. I am indebted to the late R. B. Dominick of The Wedge Plantation, whose hospitality and interest in Lepidoptera gave me access to one of the

few known habitats of this species and led to this research on it. I thank Richard L. Brown, Ray Gagné, Ronald W. Hodges, and Timothy L. McCabe for reviewing the paper.

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**AN ANNOTATED KEY AND ILLUSTRATIONS TO THE  
SPECIES OF THE GENUS *CUCULLIA*  
(LEPIDOPTERA: NOCTUIDAE: CUCULLIINAE) FROM  
MEXICO AND CENTRAL AMERICA**

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*Abstract.*—A key to the Mexican and Central American species of the genus *Cucullia* is presented. The key is annotated with the geographical distribution of each species and supplemented with illustrations of the adults of each species.

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Jack Franclemont, among his many and diverse interests, has always had a special affection for the species of the genus *Cucullia* Schrank. The species in *Cucullia* have a characteristic long, pointed forewing and the patagia are raised into a pointed hood. Although these two features are not unique to *Cucullia*, the species of the genus are usually easily recognizable. The genus is primarily Holarctic with the bulk of its diversity in Europe, North America, and Asia. Species are relatively less well represented in Africa. The genus is strongly developed in Canada and the United States, but much more poorly represented south of the U.S.–Mexican border. The southernmost known extension of the genus is in Costa Rica. Only a single species occurs in Mexico and Central America that is not found in the United States, *Cucullia costaricensis* Hampson. I have recently completed a revision of the genus *Cucullia* which will soon appear as part of a fascicle in the *Moths of America North of Mexico* series (Poole, 1992). The purpose of this paper is to complete the treatment of the New World species of the genus by presenting an annotated key and illustrations to the species known or strongly suspected to occur in Mexico and Central America. This paper is meant to supplement the *Moths of America North of Mexico* fascicle. Color illustrations of all of the species (except *costaricensis*) along with full discussions and descriptions of the species, and photographs of the male and female genitalia may be found there. References to original descriptions and dates of publication may also be found in that publication or alternatively may be retrieved from Poole (1989).

Many of the species treated are U.S. species which have not yet been collected south of the border but probably occur in northern Mexico. I have not included those species that are part of the Mohave Desert region fauna of southern California that also occur in northern Baja California. The reader will want to refer to the *Moths of America North of Mexico* fascicle for the identification of species of *Cucullia* from this region of Mexico.

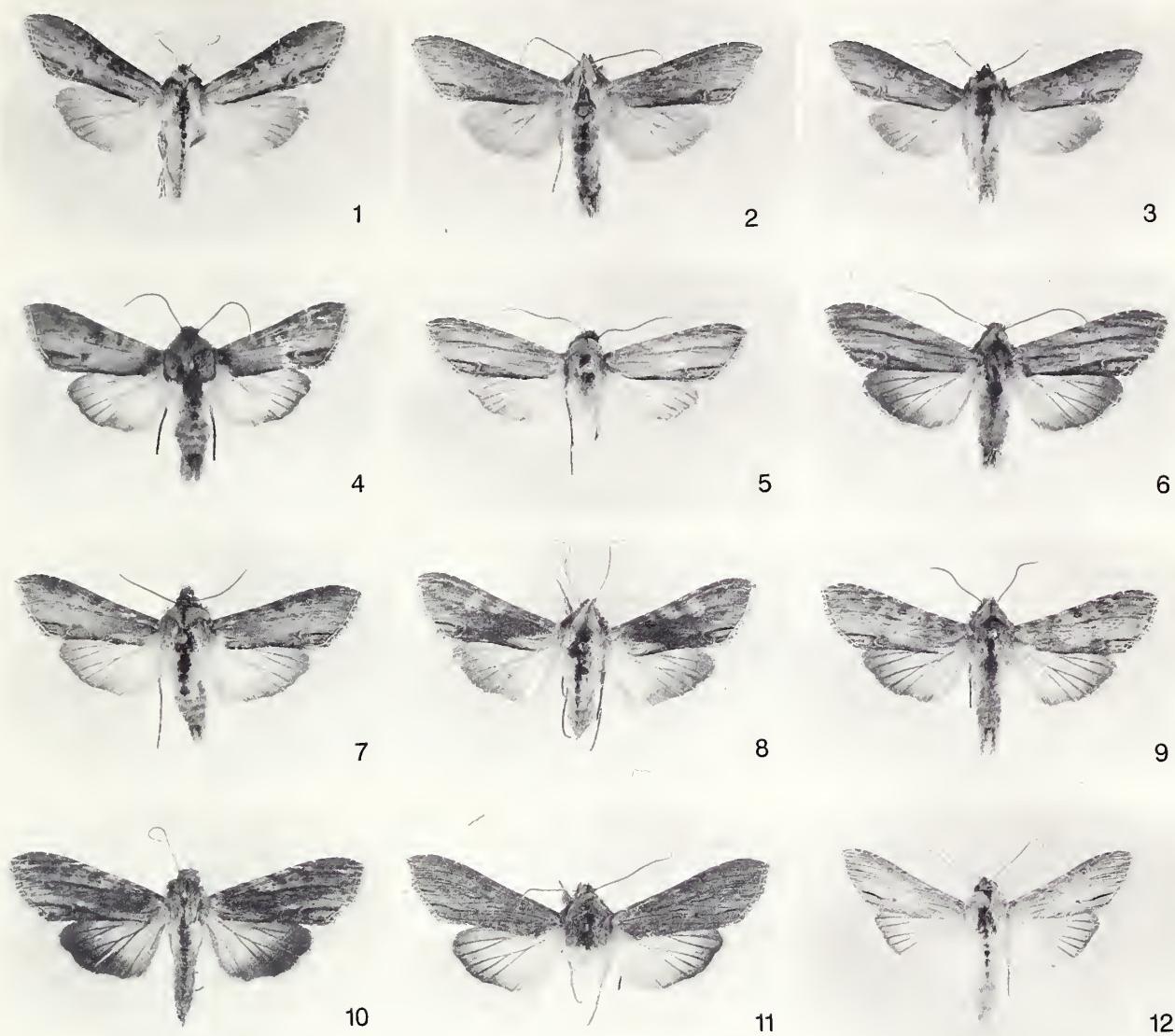
The following is a list of the species treated in this paper arranged by species groups following the arrangement in the *Moths of America North of Mexico* fascicle.

*asteris* species group  
*Cucullia montanae* Grote

- Cucullia postera* Guenée  
*Cucullia obscurior* Smith  
*convexipennis* species group  
*Cucullia lilacina* Schaus  
*Cucullia eucaena* Dyar  
*Cucullia costaricensis* Hampson  
*Cucullia oribac* Barnes  
*speyeri* species group  
*Cucullia* new species #1  
*Cucullia laetifica* Lintner  
*Cucullia* new species #2  
*Cucullia* new species #3  
*Cucullia eccissica* Dyar  
*antipoda* species group  
*Cucullia antipoda* Strecker  
*strigata* species group  
*Cucullia serraticornis* Lintner

#### KEY TO THE SPECIES OF *CUCULLIA*

1. Fore tibia with a distinct claw; front of head with large, triangular frontal process ..... *antipoda*  
*Cucullia antipoda* Strecker (Fig. 16) has not been seen from Mexico, but is abundant in the drier areas of the western United States and has been collected in southern New Mexico and Arizona. It probably will be found in Chihuahua and Sonora.
- Fore tibia without a distinct claw; front of head without frontal process ..... 2
2. Palpi studded with thin brown hairs giving palpi a bristly look; each antennal segment of male ventrally expanded into a laterally projecting plate of variable development, each plate with distinct hairs; early spring fliers ..... *serraticornis*  
*Cucullia serraticornis* Lintner (Figs. 17, 18) has not yet been collected in Mexico. It occurs commonly in southern California and in southeastern Arizona. It undoubtedly will be found in Sonora as well.
- Palpi not studded with thin brown hairs, not appearing bristly; antennal segments of male simple ..... 3
3. Lower third of postmedial line of forewing a conspicuous light line edged with black on both sides; orbicular and reniform usually obviously present; forewing not gray, but if gray usually with a distinct violet or blue tint ..... 4
- Lower third of postmedial line of forewing not conspicuous although often vaguely present; orbicular and reniform usually obscure or absent; forewing some shade of gray with or without a bluish tint, never purplish ..... 11
4. A dark lateral streak through the middle of the forewing along the cubital vein ..... 5
- No dark lateral streak through the middle of the forewing along the cubital vein ..... 6
5. Larger species (forewing length from base to apex approximately 25 mm) ..... *costaricensis* (?)  
..... *costaricensis* (?)
- Smaller species (forewing length from base to apex approximately 20 mm) ..... *oribac*  
*Cucullia oribac* Barnes (Figs. 5, 6) has been seen from Veracruz, Morelos, Chiapas, and the Federal District in Mexico. Its northern limit is southern and central Arizona

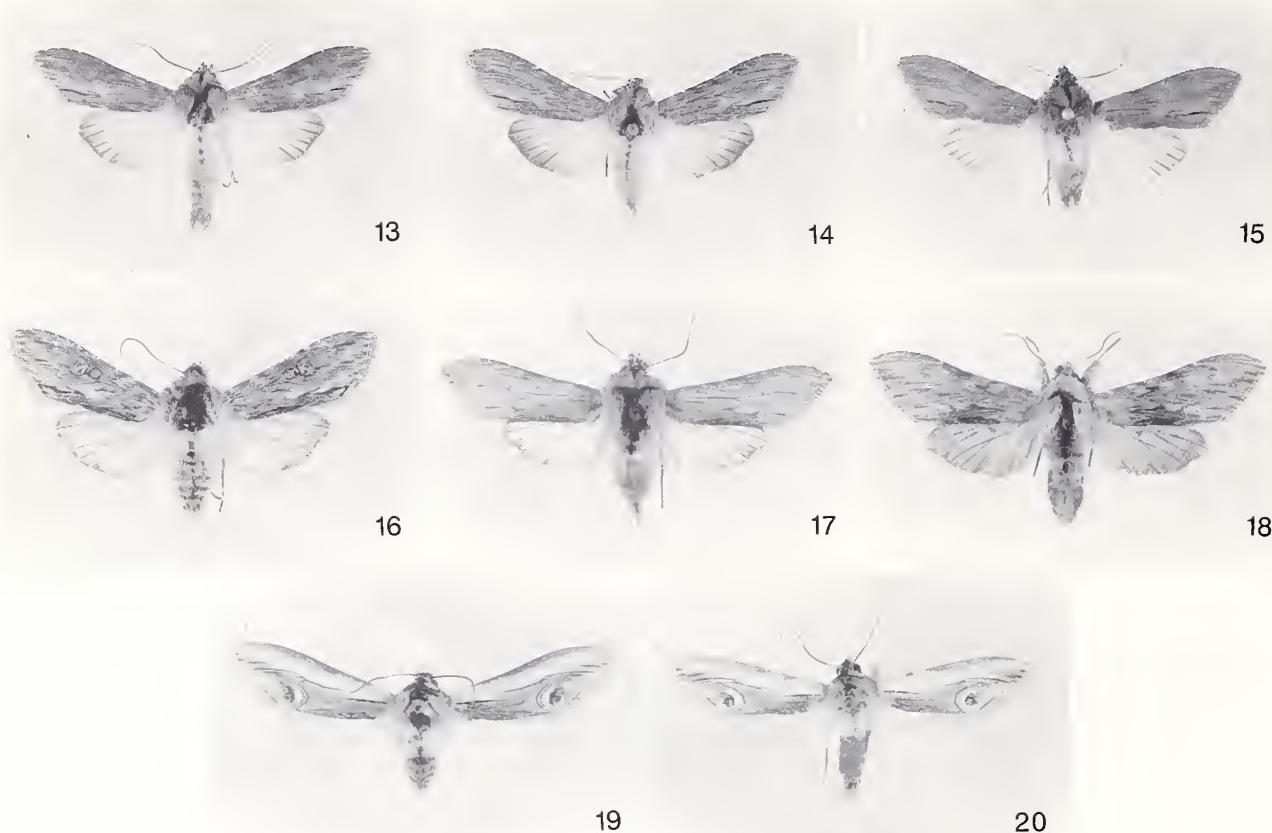


Figs. 1–12. *Cucullia* species. 1. *C. montanae* Grote, ♂, Portal, Cochise Co., Arizona, USA. 2. *C. obscurior* Smith, ♂, Alta Lakes, San Miguel Co., Colorado, USA. 3. *C. postera* Guenée, ♂, Hill City, Pennington Co., South Dakota, USA. 4. *C. lilacina* Schaus, ♂, Lomas de Chepultepec, Distrito Federal, Mexico. 5. *C. oribac* Barnes, ♂, Zacualpan, Mexico, Mexico. 6. *C. oribac* Barnes, ♀, Ciudad de Mexico, Distrito Federal, Mexico. 7. *C. eucaena* Dyar, ♂, Mount Locke, Jeff Davis Co., Texas, USA. 8. *C. eucaena* Dyar, ♀, Lomas de Chepultepec, Distrito Federal, Mexico. 9. *C. costaricensis* Hampson, ♂, Mount Poas, Alajuela, Costa Rica. 10. *C. costaricensis* Hampson, ♀, Orizaba, Veracruz, Mexico. 11. *C. new species #2*, ♂, Lomas de Chepultepec, Distrito Federal, Mexico. 12. *C. new species #1*, ♂, Hondo, Medina Co., Texas, USA.

to western New Mexico. It probably occurs generally in Mexico, possibly extending further south into Guatemala.

6. Forewing lilac or violet with a distinct fawn-brown patch between the reniform and outer margin ..... *lilacina*

The violet forewing color of *Cucullia lilacina* Schaus (Fig. 4) is very distinctive. The species has been collected in Veracruz and the Federal District in Mexico and the state of Cartago in Costa Rica. The northern limit of its range is in Arizona, New Mexico, and western Texas.



Figs. 13–18. *Cucullia* species. 13. *C. laetifica* Lintner, ♂, Irving, Dallas Co., Texas, USA. 14. *C.* new species #3, ♀, Panther Pass, Brewster Co., Texas, USA. 15. *C. eccissica* Dyar, ♂, Lomas de Chepultepec, Distrito Federal, Mexico. 16. *C. antipoda* Strecker, ♂, Ephraim, Sanpete Co., Utah, USA. 17. *C. serraticornis* Lintner, ♂, Loma Linda, San Bernardino Co., California, USA. 18. *C. serraticornis* Lintner, ♀, Loma Linda, San Bernardino Co., California, USA.

Figs. 19–20. *Opsigalea* species. 19. *O. ocellata* Walker, ♂, Lomas de Chepultepec, Distrito Federal, Mexico. 20. *O. blanchardi* Todd, ♂, Fort Davis, Jeff Davis Co., Texas, USA.

- Forewing not as above ..... 7
- 7. Hindwing pure white or with a white base and dark brown outer margin ..... 8
- Hindwing dull brown and if base lighter than outer margin, not conspicuously so ..... *obscurior*

*Cucullia obscurior* Smith (Fig. 2) has not yet been collected in Mexico, but it has been collected in extreme southern Arizona and probably occurs in northern Sonora as well.

- 8. Basal area of forewing with a large area of light brown; hindwing of male with broad band of dark brown; median and middle subterminal area of forewing contrastingly lighter than rest of wing ..... *montanae*

*Cucullia montanae* Grote (Fig. 1) has not yet been collected in Mexico, but has been seen from southern Arizona, New Mexico, and western Texas. It probably occurs in northern Sonora and Chihuahua.

- Basal area of forewing without large patches of light brown; hindwing of male (but not of female) without broad band of dark brown; median and middle subterminal area of forewing not significantly lighter than remainder of forewing ..... 9
- 9. Forewing with postmedial line distinct near costal margin; median area of male not

uniform violet-gray; male without rusty patch between reniform and apex; female with dark streak on median vein of forewing ..... *costaricensis* (♀ and ♂)

*Cucullia costaricensis* Hampson (Figs. 9, 10) is the largest and most southerly species of the genus in the New World. The only species *costaricensis* might be confused with is *eucaena*. Its larger size and superficial differences are illustrated in the plate. In the male genitalia the smaller spine of the vesica is very short, about as long as wide, but in *eucaena* the spine is at least twice as long as wide. The clasper of the valve barely exceeds the costa of the valve in *costaricensis* but greatly surpasses the costa in *eucaena*. It has been collected in the state of Veracruz in Mexico, Baja Verapaz and Quezaltenango in Guatemala, and San Jose, Cartago, and Alajuela in Costa Rica.

- Forewing with postmedial line indistinct near costal margin; median area of male uniform purple-gray; male with rusty patch between reniform and apex; female without dark streak on median vein of forewing ..... 10
- 10. Forewing with small patch of white scales at base of forewing; male genitalia with clasper medially placed in valve; ductus bursae of female genitalia without knob at caudal end ..... *eucaena*

*Cucullia eucaena* Dyar (Figs. 7, 8) is known from Puebla, Veracruz, Guerrero, and the Federal District in Mexico. As in *costaricensis* and *oribac* the sexes are strongly dimorphic. The male of *eucaena* is almost identical to *postera* from southern Arizona. The white spot at the base of the forewing should identify it, but the male genitalia may need to be checked to be sure. The female is suffused with dark brown, but the female of *postera* is similar to the male.

- Forewing without a small patch of white scales at base of forewing; male genitalia with clasper distally placed in valve; ductus bursae of female genitalia with knob at caudal end ..... *postera*

*Cucullia postera* Guenée (Fig. 3) is primarily a species of the northern parts of the United States and most of Canada. It also occurs throughout the Rocky Mountain region and has been taken near the Mexican border in southern New Mexico. It has not yet been collected in Mexico, but probably will be. The male is almost identical to the male of *eucaena* except for the small white patch mentioned in the key. For certainty the male genitalia must be checked. Females resemble the males unlike the female of *eucaena*.

- 11. Forewing very light gray with central median area almost white; black dash on lower fourth of postmedial line contrasting with light coloration of median area ..... new species #1

*Cucullia* new species #1 (Fig. 12) has not yet been collected in Mexico, but occurs throughout eastern and central Texas south to Brownsville and is commonest along the coast. It probably occurs in Tamaulipas and possibly Nuevo Leon as well. The light gray tinted with white coloration of the forewing will separate it from *laetifica*.

- Forewing not as above ..... 12
- 11. Forewing uniform dark black-gray; claspers of right and left valves of male genitalia equal in size; vesica of aedeagus with two spines ..... new species #2

*Cucullia* new species #2 (Fig. 11) is the largest and darkest species of the *speyeri* species group. It has been collected in the Federal District of Mexico. Elsewhere it is known only from southeastern Arizona. Its largest size and dark coloration will distinguish it from the other species in the *speyeri* species group.

- Not as above ..... 13

13. Forewing with a light patch in the median area; forewing with a slightly metallic blue tint ..... *laetifica*

*Cucullia laetifica* Lintner (Fig. 13) has not yet been collected in Mexico. The species is common in southern Arizona, New Mexico, and Texas and undoubtedly occurs throughout northern Mexico as well.

- Forewing without a light patch in the median area; forewing uniformly light gray without a metallic blue tint ..... 14  
13. Vesica of male genitalia with two spines ..... *eccissica*

*Cucullia eccissica* Dyar (Fig. 15) has been collected in the states of Puebla and Mexico in Mexico. In the United States it occurs in southern California and southern Arizona.

- Vesica of male genitalia with three spines ..... new species #3

*Cucullia* new species #3 (Fig. 14) has not been collected in Mexico as yet, but occurs in western Texas and southern Arizona and probably occurs in Coahuila, Chihuahua and Sonora as well. Its smaller size and the three spines in the vesica will distinguish it from *eccissica*.

In addition to the species of *Cucullia* keyed above, there are two species of the genus *Opsigalea* Hampson occurring in Mexico that may be mistaken for species of *Cucullia*. These two species are *Opsigalea ocellata* (Walker) (Fig. 19) and *Opsigalea blanchardi* Todd (Fig. 20).

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## A REVISION OF THE GENUS *HYPSOROPHA* HÜBNER (LEPIDOPTERA: NOCTUIDAE: OPHIDERINAE)

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*Abstract.*—The genus *Hypsoropha* (Lepidoptera: Noctuidae) is revised and two new species, *H. franclemonti*, and *H. baja* are described. Male and female genitalia and adult habitus are illustrated for all known species in the genus. Character states and resulting cladogram are presented.

*Hypsoropha* Hübner (Lepidoptera: Noctuidae: Ophiderinae) is a genus known from Middle and North America. Two of the included species, *H. monilis* Fabricius (1777) and *H. hormos* Hübner (1818) are common in the southeastern United States. *Hypsoropha adeona* Druce (1889) was described from Mexico and has recently been recorded from Costa Rica by Daniel H. Janzen (in collection of J. G. Franclemont and USNM). A fourth species is herein recorded from Cuba and the Bahamas and a fifth from Mexico and Arizona. The only other species previously associated with the genus, *Tiauspa* [*Hypsoropha*] *argyria* Butler (1879), was transferred from the Noctuidae and made the type of a notodontid genus, *Ctianopha*, by Schaus (1901).

Both *Hypsoropha monilis* and *H. hormos* range over most of the southeastern United States with *H. hormos* being the most widespread, having been reported as far west as Arizona (Forbes, 1954), and as far north as New Hampshire and New York (Crumb, 1956). *Hypsoropha hormos* larvae feed on Persimmon (*Diospyros virginiana* L.) [Ebenaceae] (Dyar, 1899; Glover, 1878; Gueneé, 1852) and Sassafras (*Sassafras albidum* (Nutt.)) Nees [Lauraceae] (Forbes, 1954). *H. monilis* larvae have been reported from *Diospyros* (Crumb, 1956) and I have seen larvae (Fig. 29) from New Jersey on *D. virginiana*.

### *Hypsoropha* Hübner, 1818

Type species: *Noctua monilis* Fabricius by subsequent designation by Grote, 1874.  
*Gloee* Hübner, 1808, suppressed (ICZN Op. 789).

Type species: *Gloee monilis* sensu Hübner by subsequent designation by Berio, 1957.

### *Euphais* Hübner, 1818.

Type species: *Noctua monilis* Fabricius by subsequent designation by Berio, 1957.  
*Monogona* Gueneé, 1852.

Type species: *Hypsoropha hormos*, by monotypy.  
*Tiauspa* Walker, 1858.

Type species: *Hypsoropha hormos*, by monotypy.

Gloce Neave, 1939, mispelling.

Description: Palpus upturned beyond vertex in males; male antenna pectinate to subpectinate, female antenna filiform; eyes naked; reniform inconspicuous or absent; orbicular a black point; forewing apex slightly falcate; female possessing appendix bursa.

*Hypsoropha*'s monophyly is established by the following synapomorphies: forewing with a transverse series of about four circular white markings in the fold along the postmedian line; 8th abdominal sternum in the male with a peculiar pincer-like development.

The nearest relatives appear to belong to the genus *Psammathodoxa* as suggested by Franclemont (1985). *Psammathodoxa* and *Hypsoropha* share a chitinized development of the eighth abdominal sternum, although this has become much more elaborate in the latter.

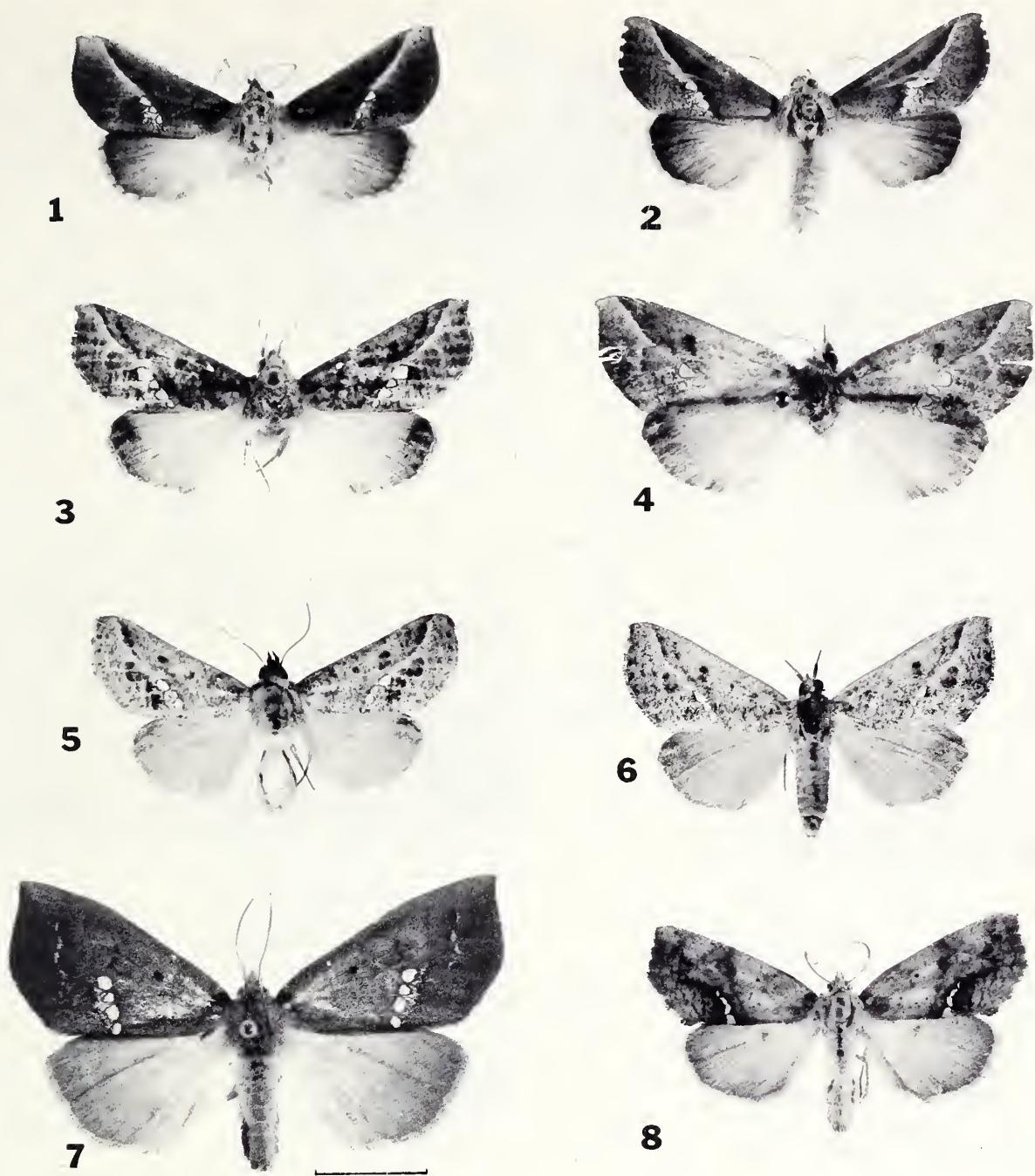
### ***Hypsoropha franclemonti*, new species**

Description. Antenna pectinate in male, simple in female; palpus upturned beyond vertex in male, to middle of front in female; head, tegula and thorax violet-gray; forewing with even, oblique postmedian line starting as four white markings in fold and terminating at costa near apex; antemedian line, when traceable, bowed out at middle; reniform obscure, orbicular a black point; wings silvery gray with diffuse whitish scaling along posterior margin and at apex; hindwing buff from base to middle, gradually darkening toward margin; fringe white. Male genitalia and eighth sternite as in Figures 10 and 12. Female genitalia as in Figure 9. Expanse 25–34 mm.

Diagnosis. *H. franclemonti* can be distinguished from *H. monilis* and *H. hormos* by the even, oblique postmedian line; from *H. adeona* and *H. baja* by the buff-gray hindwing and less mottled forewing. The female bursa copulatrix has one band of signa in *H. franclemonti* versus two bands in *H. adeona*. Other structural differences in genitalia are evident from the illustrations (compare Figs. 9–12, 13–16, and 25–28). *Hypsoropha franclemonti* is presently known only from Cuba and Great Exuma Island in the Bahamas. *Diospyros crassinervis* (Krug & Urb.) Standl. has been reported in Cuba as well as in the Bahamas (Correll and Correll, 1982) and may prove to be an acceptable food plant for the new species.

Type material. **BAHAMAS**, Holotype male: Great Exuma Island, Simon's Point, lat 23.31.50 long. 75.47.30, 11 April 1986, T. L. McCabe [NYSM]; Paratypes, 17: **CUBA** (2) Santiago (no additional data) [USNM, BMNH]; and the **BAHAMAS** (14) (same data as Holotype except dates run from 10–16 April 1986) [NYSM, LACM, JGF]; Bahamas: J. M. St. J. Yates (no additional data) (1) [BMNH]. Paratypes will be deposited in the USNM, the BMNH, the LACM, and the collection of J. G. Franclemont.

It gives me great pleasure to name this species after Prof. John G. Franclemont. I have benefitted greatly from his frequent counsel. It seems especially fitting to commemorate him with a species in a group for which a connection had been made through his knowledge and insight.

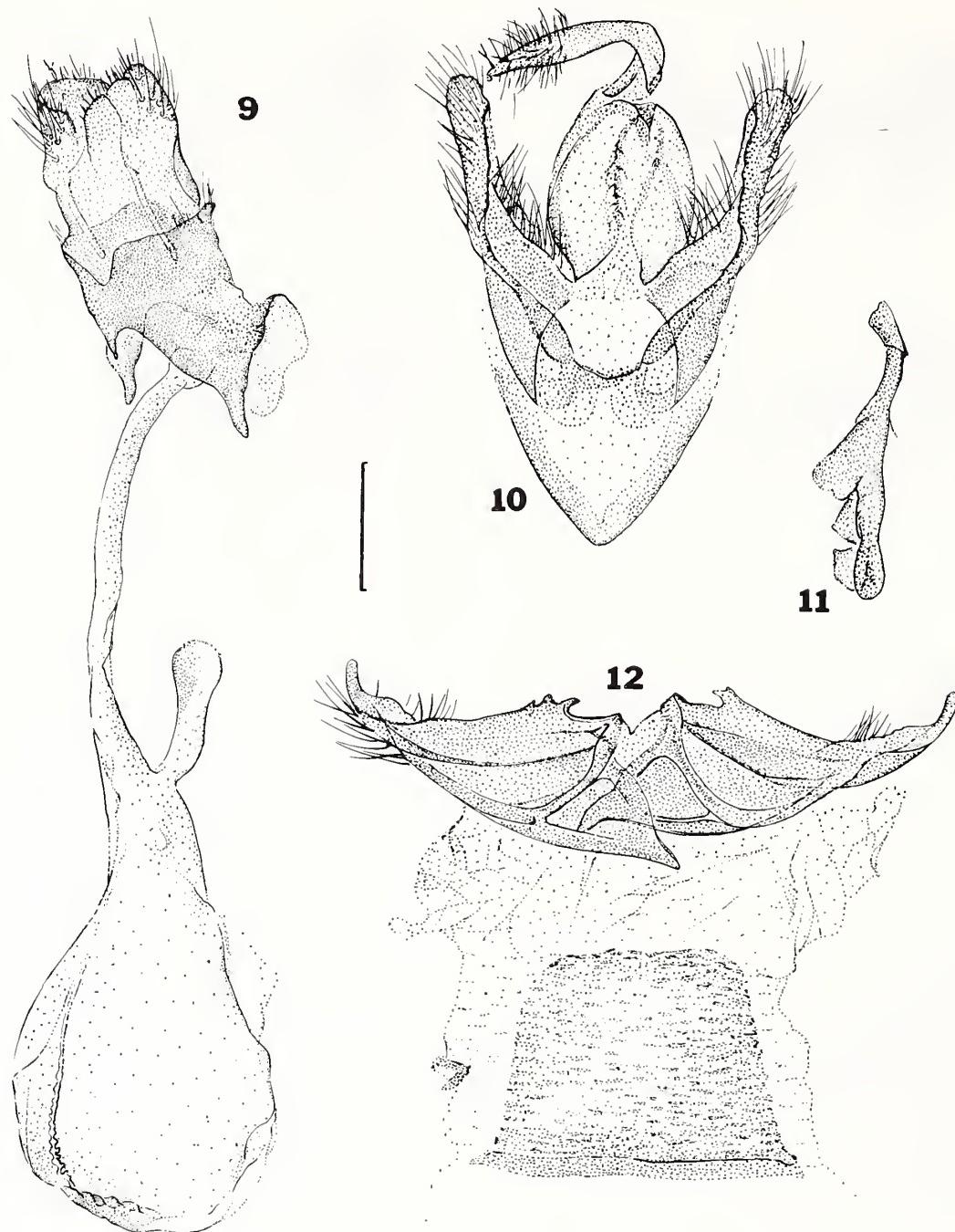


Figs. 1-8. 1. *Hypsorpha franclemonti*, Holotype male, Bahamas, 15 April 1986. 2. *H. franclemonti*, Paratype female, same data. 3. *H. adeona*, male, Guanacoste, Costa Rica. 4. *H. adeona*, female, Veracruz, Mexico. 5. *H. baja*, Holotype male, Baja California, 10-11 Sept. 1984. 6. *H. baja*, Paratype female, same locale, 9 Sept. 1984. 7. *H. monilis*, male, Liberty Co., Florida, 25 March 1983. 8. *H. hormos*, male, Alachua Co., Florida, 3 April 1986. Scale line 10 mm.

#### *Hypsorpha baja*, new species

Figs. 5, 6, 25-28

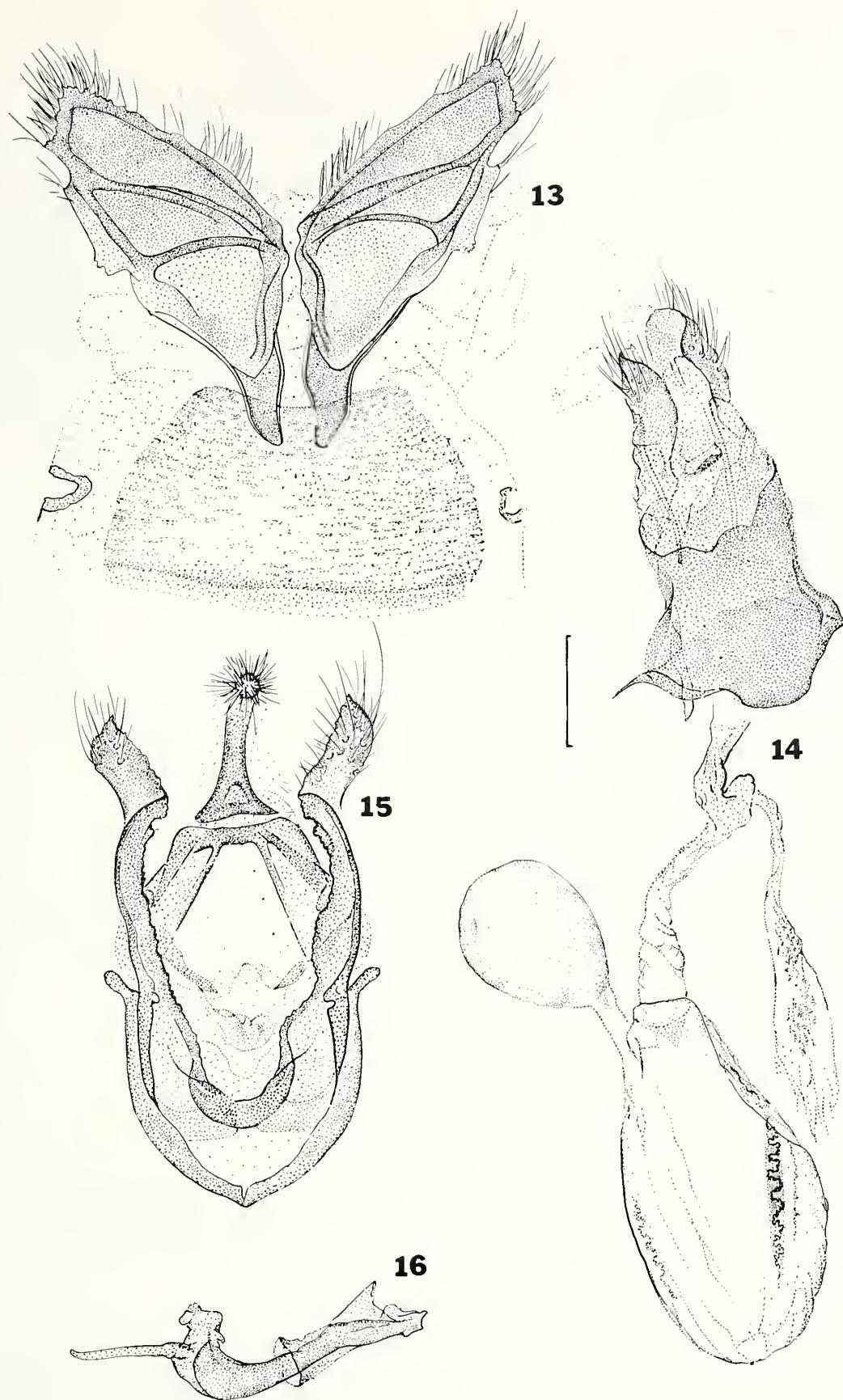
Description. Antenna pectinate in male, simple in female; palpus upturned beyond vertex in male, to middle of front in female; head, tegula and thorax violet-gray; forewing with even, oblique postmedian line starting as four white markings in fold and terminating at costa near apex; antemedian line, when traceable, bowed out at



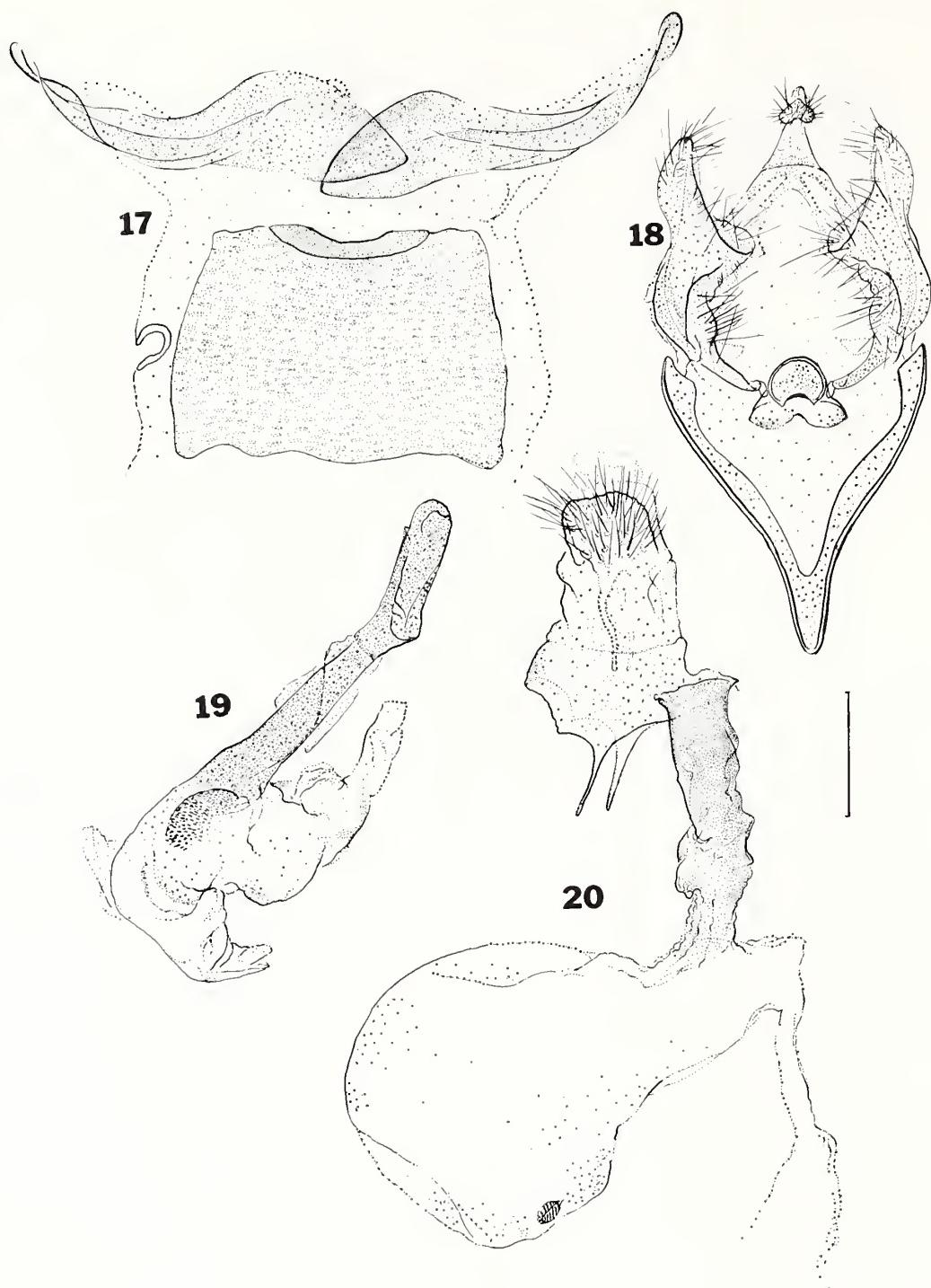
Figs. 9–12. *Hypsoropha franclemonti*. 9. Female genitalia (ventral view), McCabe slide 1499, Bahamas, 10 April 1986. 10. Male genitalia, McCabe slide 1497, Bahamas. 11. Aedeagus with vesica unevected, McCabe slide 1497, Bahamas. 12. Seventh and eighth abdominal sterna, McCabe slide 1497, Bahamas. Scale line 1 mm.

middle; reniform obscure, orbicular a black point; wings brownish gray with diffuse whitish scaling at apex, heavily mottled; hindwing buff from base to middle, slight darkening toward margin; fringe white. Male genitalia and eighth sternum as in Figures 26–28. Female genitalia as in Figure 25. Expanse 29–35 mm.

**Diagnosis.** *H. baja* can be distinguished from *H. franclemonti* by the more irrorated forewings and male eighth sternites that lack teeth, and from *H. adeona* by the smaller size and gray hindwings (creamy in *H. adeona*). *H. baja* has a variable am line (absent to well represented whereupon it is dentate across from cell) and a variable amount of freckling (almost smooth in one specimen). It is presently known only from the



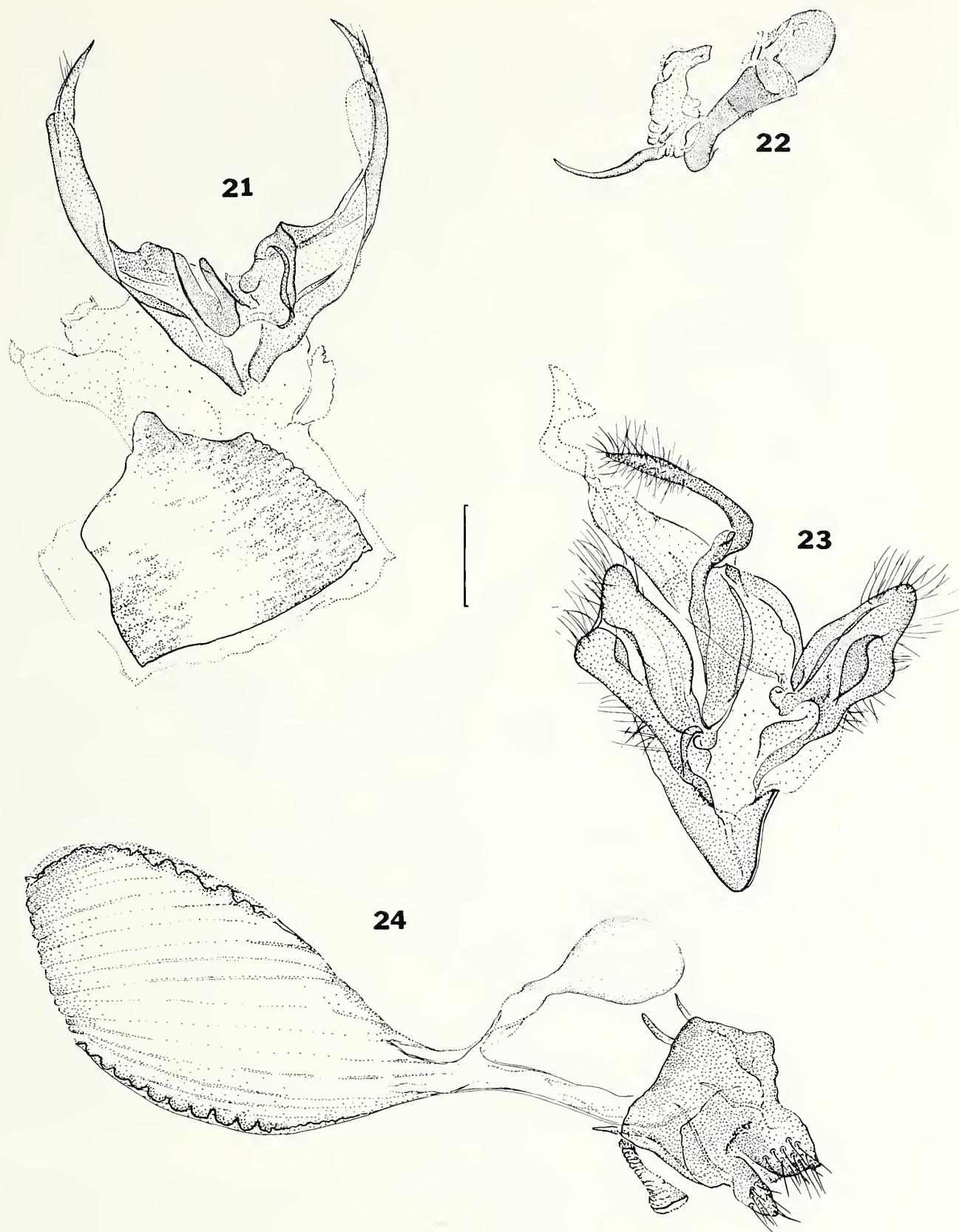
Figs. 13–16. *Hypsorpha adeona*. 13. Seventh and eighth abdominal sterna, McCabe slide 1515, Guanacaste, Costa Rica. 14. Female genitalia (ventral view), McCabe slide 1514, Veracruz, Mexico. 15. Male genitalia, same data as Figure 13. 16. Aedoeagus with vesica everted, same data as Figure 13. Scale line 1 mm.



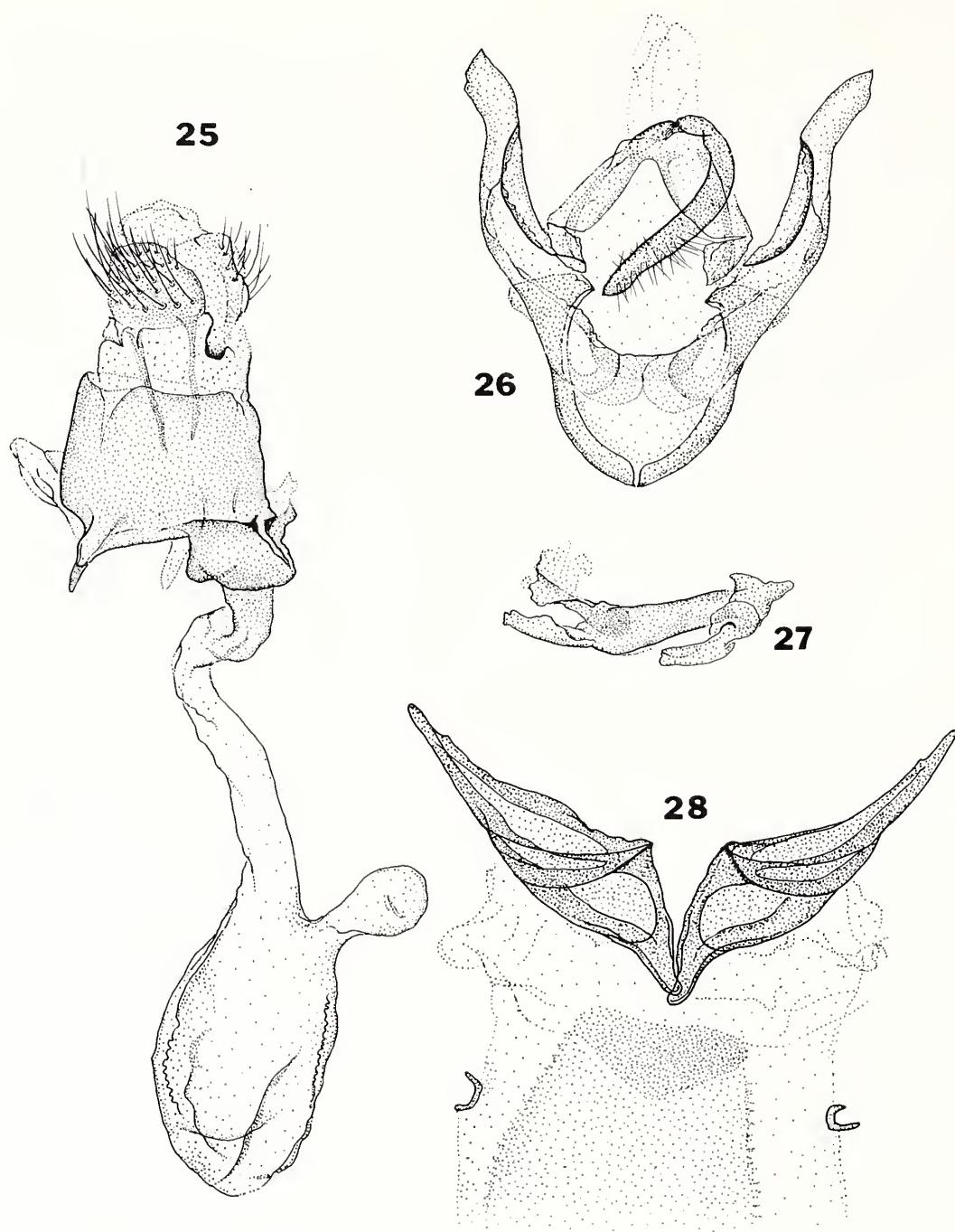
Figs. 17–20. *Hypsorpha monilis*. 17. Seventh and eighth abdominal sterna, McCabe slide 1513, Alachua Co., Florida, 28 March 1986. 18. Male genitalia, same data as Figure 17. 19. Aedeagus with vesica everted, same data as Figure 17. 20. Female genitalia (ventral view), McCabe slide 1405, Alachua Co., Florida, 30 March 1986. Scale line 1 mm.

Baja and Arizona. *Diospyros californica* (Brandegee) I. M. Jhtn. has been reported in the Baja (Wiggins, 1980) and may prove to be an acceptable food plant for this new species.

Type material. MEXICO, Holotype male: Baja Calif. Sur Cabo Pulmo, sea level, 10–11 September 1984, J. P. & K. E. Donahue [LACM]. Paratypes, 10: MEXICO: same data as holotype [5 specimens—LACM, NYSM]; Mexico: Baja Ca Sur, 12 mi S P. Colorado, Arroyo Las Barracae, 15–18 Oct 1989, N. Bloomfield [1-LACM]; Mexico: Colima, 13 mi N Manzanillo, nicr. Toro 24–26 May 1989 N. Bloomfield [1-LACM] Aguaje, Sinaloa, Mex., VI-18 1956, R. P. Allen [1-CAS]; Baja Calif., San



Figs. 21-24. *Hypsoropha hormos*. 21. Seventh and eighth abdominal sternites, McCabe slide 1491, Alachua Co., Florida, 3 April 1986. 22. Aedeagus with vesica everted, same data as Figure 21. 23. Male genitalia, same data as Figure 21. 24. Female genitalia (dorsal view), McCabe slide 1404, Alachua Co., Florida, 27 March 1986. Scale line 1 mm.



Figs. 25–28. *Hypsorophha baja*. 25. Female genitalia (ventral view), McCabe slide 1769, Baja, California, 24 July 1981. 26. Male genitalia, McCabe slide 1787, Baja, California, 24 July 1981. 27. Aedoeagus, same data as Figure 26. 28. Seventh and eighth abdominal sternites, same data as Figure 26.

Bartola Microwave Tower, 2000 ft., July 24, 1981, R. Holland [1-AMNH]. UNITED STATES: Arizona: August 22, 1954, Madera Canyon, Santa Rita Mts., Southern Arizona, Lloyd M. Martin [1-LACM].

*Hypsorophha adeona* Druce  
Figs. 3–4, 13–16

*Hypsorophha adeona* Druce, 1889:338, pl. 30, fig. 28.  
*Hypsorophha adeona*; Poole, 1989:546.

Table 1. Character states.

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1. Male eighth sternum: narrow (0), flattened (1); expanded (2).
  2. Male eighth sternum with supporting struts: absent (0); present (1).
  3. Male antennae: heavily pectinate (0); subpectinate (1).
  4. Valves with fold: central (0); marginal (1).
  5. Male eighth sternum with teeth: absent (0); present (1).
  6. Pm line: straight (0); indented (1).
  7. Forewing white markings: absent (0); present (1).
  8. Saccus a "V" (0); a "U" (1).
  9. Female ductus bullae broad and chitinized (1) or not (0).
  10. Female bursal bands/signa: two bands (0); one band (1); one signum (2).
  11. Female appendix bursae: absent (0); weakly developed (1); well developed (2).
  12. Female with mid-ventral chitinized pocket between ovipositor lobes: absent (0); present (1).
  13. Eight sternite directed: posteriorly (0); anteriorly (1).
  14. Aedoeagus a narrow, curved tube (0) or broad and straight (1).
  15. Uncus: simple (0); slightly modified (1); keel-shaped (2).
  16. Cucullus: absent (0); present (1).
  17. Forewing with circular markings: absent (0); present (1).
  18. Postmedian line: broken (0); entire (1).
- 

Description. Antenna subpectinate in male, simple in female; palpus upturned beyond vertex in both sexes; head, tegula and thorax buff with yellowish tint; forewing with even, oblique postmedian line starting as four white markings in fold and terminating at costa near apex; antemedian line, when traceable, bowed out opposite cell; reniform obscure, orbicular a black blotch; wings yellow-brown and heavily mottled; hindwing with basal two thirds yellow, gradually darkening toward margin; fringe brown. Male genitalia and eighth sternum as in Figures 15 and 13. Female genitalia as in Figure 14. Expanse 35–40 mm.

Diagnosis. Both *H. adeona* and *H. franclemonti* possess the even, oblique postmedian lines, but *H. franclemonti* has a buff-gray hindwing (see diagnosis under *H. franclemonti*). The moth occurs from Mexico to Costa Rica and the food plant is unknown.

Type locality. Mexico [Veracruz], Jalapa [BMNH].

*Hypsorophha monilis* (Fabricius)  
Figs. 7, 17–20

*Noctua monilis* Fabricius, 1777:283.

*Hypsorophha monilis*; Hübner, 1816:249; *Hypsorophha monilis*; Walker, 1857:994; *Hypsorophha monilis*; Dyar, 1903:219; *Hypsorophha monilis*; McDunnough, 1938: 125; *Hypsorophha monilis*; Franclemont and Todd, 1983:123; *Hypsorophha monilis*; Poole, 1989:546.

Description. Antenna pectinate in male, simple in female; palpus upturned beyond vertex in both sexes; head, tegula and thorax orange-brown; forewing with postmedian

Table 2. Character matrix.

Taxa	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>H. adeona</i>	2	1	1	1	1	0	1	0	0	0	2	1	1	0	1	1	1	0
<i>H. baja</i>	2	1	1	1	0	0	1	0	1	0	2	1	1	0	0	1	1	0
<i>H. franclemonti</i>	2	1	0	0	1	0	1	1	0	1	2	0	1	1	0	0	1	0
<i>H. hormos</i>	1	0	0	0	0	1	1	1	0	0	2	1	1	1	0	0	1	1
<i>H. monilis</i>	1	0	0	1	0	1	1	1	1	2	1	0	1	0	2	0	1	1
<i>P. natadoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

line indented below reniform, starting as four white markings in fold and terminating at costa near apex; antemedian line rather evenly excurved when traceable; reniform obscure, orbicular a black point; wings orange-brown; hindwing orange-brown, slightly darker toward margin; fringe concolorous with ground. Male genitalia and eighth sternum as in Figures 18 and 17. Female genitalia as in Figure 20. Expanse 33–44 mm.

**Diagnosis.** *H. monilis* is distinguished from *H. adeona* and *H. franclemonti* by the indented postmedian line. A spade-shaped juxta represents an autapomorphy for *H. monilis*. The species occurs from northern Florida north to North Carolina, Illinois, and Missouri (Forbes, 1954). The larva feeds on *Diospyros virginiana* and has been described by Dyar (1903a). The head has a conspicuous, rounded, black spot which extends from the posterior margin to along the adfrontals for half their length. The dorsum is black with a pale middorsal stripe, then a subdorsal pale stripe, this followed by a black stripe (Fig. 29). *H. monilis* larvae are sawfly mimics, but spend the daytime hidden at the base of the tree, and large numbers of larvae climb at dusk onto usually one or two limbs (D. F. Schweitzer, pers. comm.). The larva diapauses as a prepupa in a weak cocoon.

**Type locality.** “Anglia” [in error for North America]. The type has not been located, but it was illustrated by Westwood (1854) on plate 54, figure 61b (plate labelled “doubtful British species”).

#### *Hypsoropha hormos* Hübner

Figs. 8, 21–24

*Hypsoropha hormos* Hübner, 1818:10, figs. 27, 28.

*Monogona hormos*: Gueneé, in Boisduval and Gueneé, 1852:402.

*Tiauspa hormos*: Walker, 1857:995.

*Hypsoropha hormos*: Dyar, 1903b:219; *Hypsoropha hormos*; McDunnough, 1938: 125; *Hypsoropha hormos*; Franclemont and Todd, 1983:123; *Hypsoropha hormos*; Poole, 1989:546.

**Description.** Antenna pectinate in male, simple in female; palpus upturned beyond vertex in both sexes; head, tegula and thorax pearl-gray; forewing with postmedian line indented below reniform, starting as four white markings in fold and terminating at costa near apex; antemedian line bowed out at middle; reniform obscure, orbicular a black point; wings pearl gray with black scaling along postmedian line; median area



Fig. 29. Last instar larva of *Hypsoropha hormos*, Bear Swamp East, Cumberland Co., New Jersey (shown on leaf of *Diospyros virginiana*).

and apex lighter gray; hindwing uniform gray-buff gradually darkening toward margin; fringe concolorous with ground. Male genitalia and eighth sternum as in Figures 23 and 21. Female genitalia as in Figure 24. Expanse 22–32 mm.

**Diagnosis.** *H. hormos* is readily distinguished from *H. adeona* and *H. franclemonti* by the indented postmedian line; from *H. monilis* by the gray color and black scaling along the postmedian line and much smaller size. A pointed male eighth sternum represents an autapomorphy for *H. hormos*. The species occurs from the Florida Keys west to Arizona (Forbes, 1954) and north as far as New Hampshire and New York (Crumb, 1956). The larva was described and the food plant, *Diospyros*, was recorded by Crumb (1956). The larva has a reticulate head pattern. A green and a brown color phase occur; the green phase has purplish spots subdorsally, these being fused on segment five and eight. The mandible has a mesal tooth. Adults show much more brown overall in the northern parts of their range.

**Type locality.** Georgia [type deposition unknown].

#### PHYLOGENETIC ANALYSIS

Polarization of character states was accomplished by outgroup comparison with *Psammothodoxa natadooides* Franclemont, which has been recognized as a near relative of *Hypsoropha* (Franclemont, 1985). The Hennig 86 computer program (Farris, 1988) was employed. The cladogram in Figure 30 is the most parsimonious tree possible for the data presented. The tree exhibited a consistency of 0.786.

Not immediately evident from the bi- and tri-state partitioning of characters is a

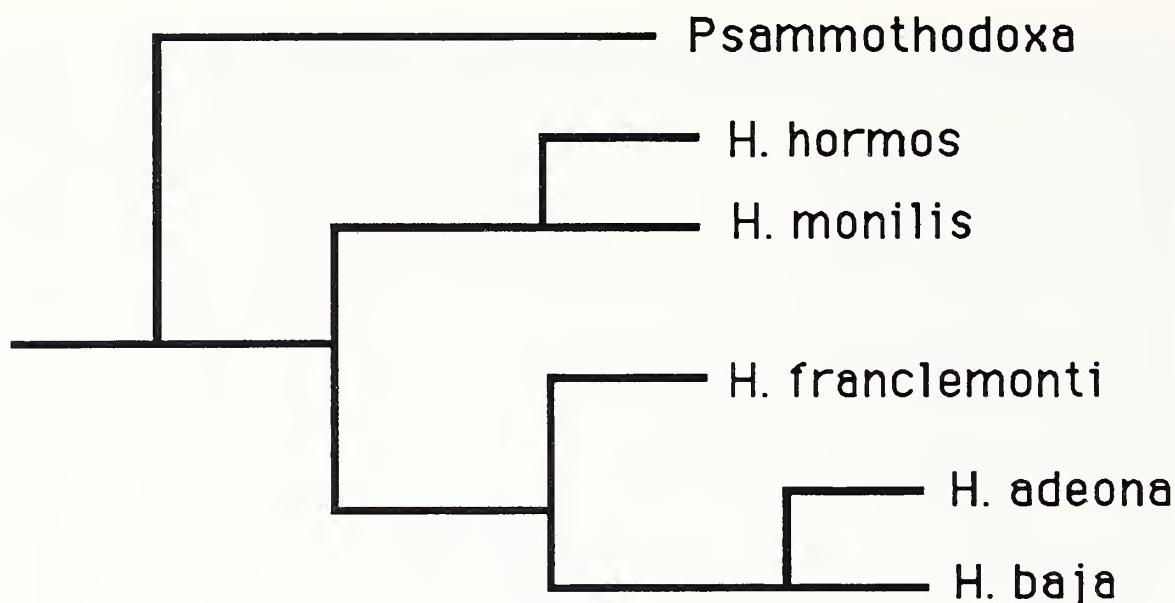


Fig. 30. Cladogram.

phytic series: the eighth abdominal sternite in the male progresses from a simple, thin, modified pincer in *H. hormos*, to a slightly heavier pincer in *H. monilis*, to an even heavier and expanded pincer in *H. franclemonti* and *H. baja* and finally to a very heavy, expanded structure in *H. adeona*. *Hypsoropha hormos*, which has the largest known distribution, is hypothesized to be the least derived species in the genus.

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LIFE HISTORY AND SYSTEMATICS OF THE  
WEST ANDEAN MOTH *AUCULA FRANCLEMENTI* WITH  
DESCRIPTION OF A NEW SPECIES FROM ECUADOR  
(LEPIDOPTERA: NOCTUIDAE: AGARISTINAE)

JOHN E. RAWLINS

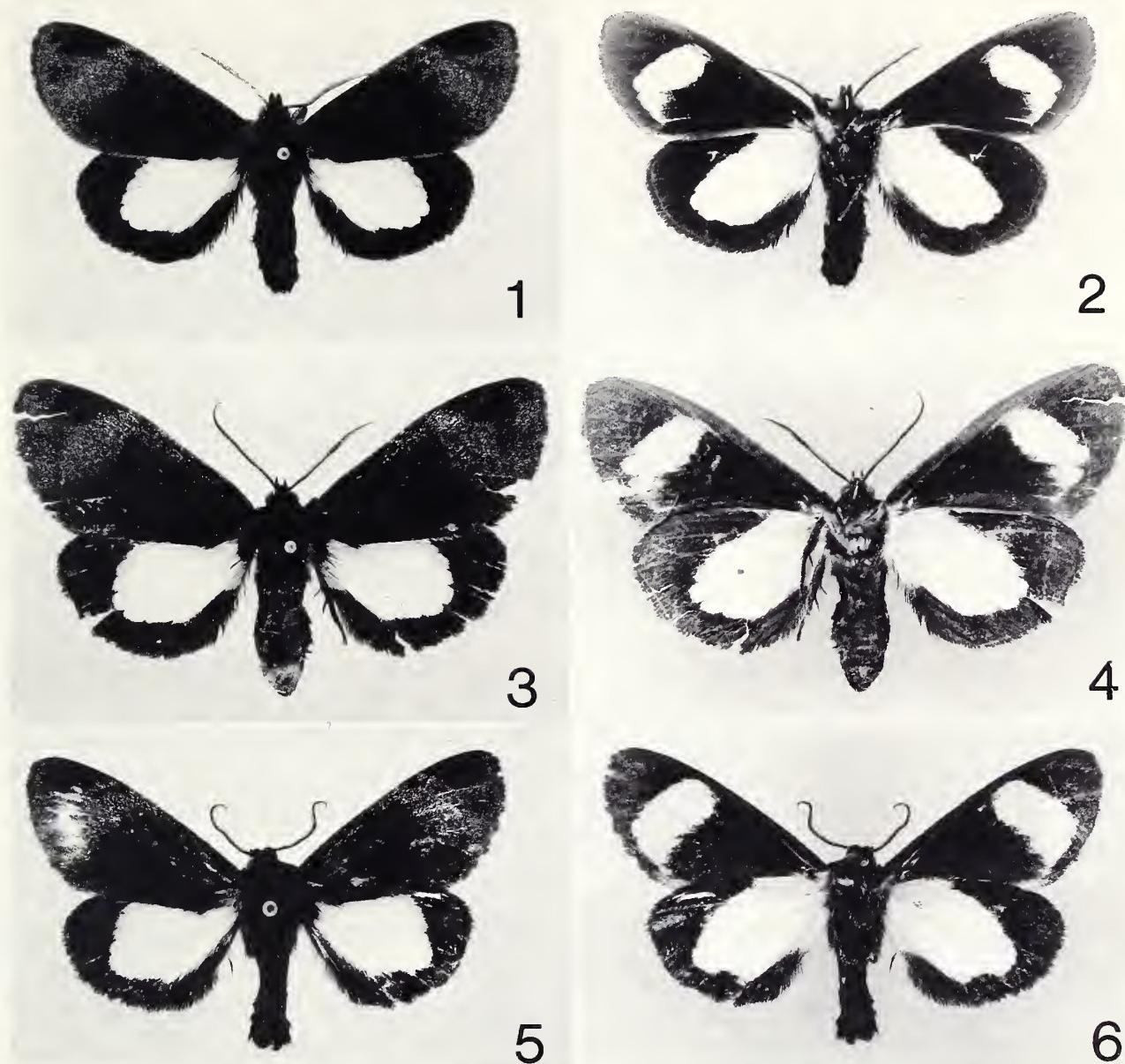
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*Abstract.*—Systematics, biology, and morphology of the rare South American agaristine moth, *Aucula franclementi* Todd and Poole (Lepidoptera: Noctuidae), are presented in the context of other agaristine genera. *A. kimsa* Todd and Poole is placed in synonymy with *A. franclementi*, and *A. ivia* Todd and Pool is synonymized with *A. tusora* Todd and Poole; *A. franclementoides*, new species, is described from east Andean Ecuador. A brief phylogenetic analysis of the five species in the *A. franclementi* species-group is offered, with a key to the species-group based on male genitalia. Female genitalia of *A. franclementi* are described, and an external mating plug (sphragis) noted, perhaps functionally related to a permanently everted and sclerotized endophallus in males. Larvae were found feeding on *Vitis tiliifolia* Humb. & Bonpl. (Vitaceae), and all immature stages reared from the egg are briefly described. A complete chaetotaxy of the last instar larva is illustrated in detail. Modifications of the pupal cremaster and the presence of subventral seta SV2 on the seventh abdominal segment are apomorphic features shared only with other agaristine species.

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Species of *Aucula* are infrequently encountered agaristine moths found in semiarid to mesic habitats in Panama and tropical South America. Kiriakoff (1977) summarized the taxonomic status of species described by earlier workers. In 1981, Todd and Poole revised *Aucula*, thoroughly describing adult males and providing a key to all species based on the male genitalia. They recognized as valid three previously described species, transferred two species to related monobasic genera (*Arpia* Schaus and *Darsetina* Felder), and excluded three species from *Aucula*, leaving them temporarily in generic combinations as originally described. They also described 21 new species based primarily on genitalic differences after examining slightly more than 100 male specimens in the following collections: National Museum of Natural History, Washington, D.C. (NMNH); The Natural History Museum, London (BMNH); Universidad Central de Venezuela; Zoologische Sammlung des Bayerischen Staates, Munich; and Carnegie Museum of Natural History, Pittsburgh (CMNH). Of the 24 species currently considered valid (Poole, 1989), nine are known from unique types, and only seven species are known from more than five specimens. The longest series for any species is 18 specimens (*Aucula ivia* Todd and Poole), 13 of which are from the same locality. Todd and Poole mentioned only 12 female specimens associated with six species but did not figure adult females or their genitalia.

A series of 23 males and two females of *A. franclementi* Todd and Poole were collected at a single locality in western Ecuador during the summer of 1983. *A. franclementi* was previously known only from the holotype. This material constitutes the largest known series of any *Aucula* species, providing information on character

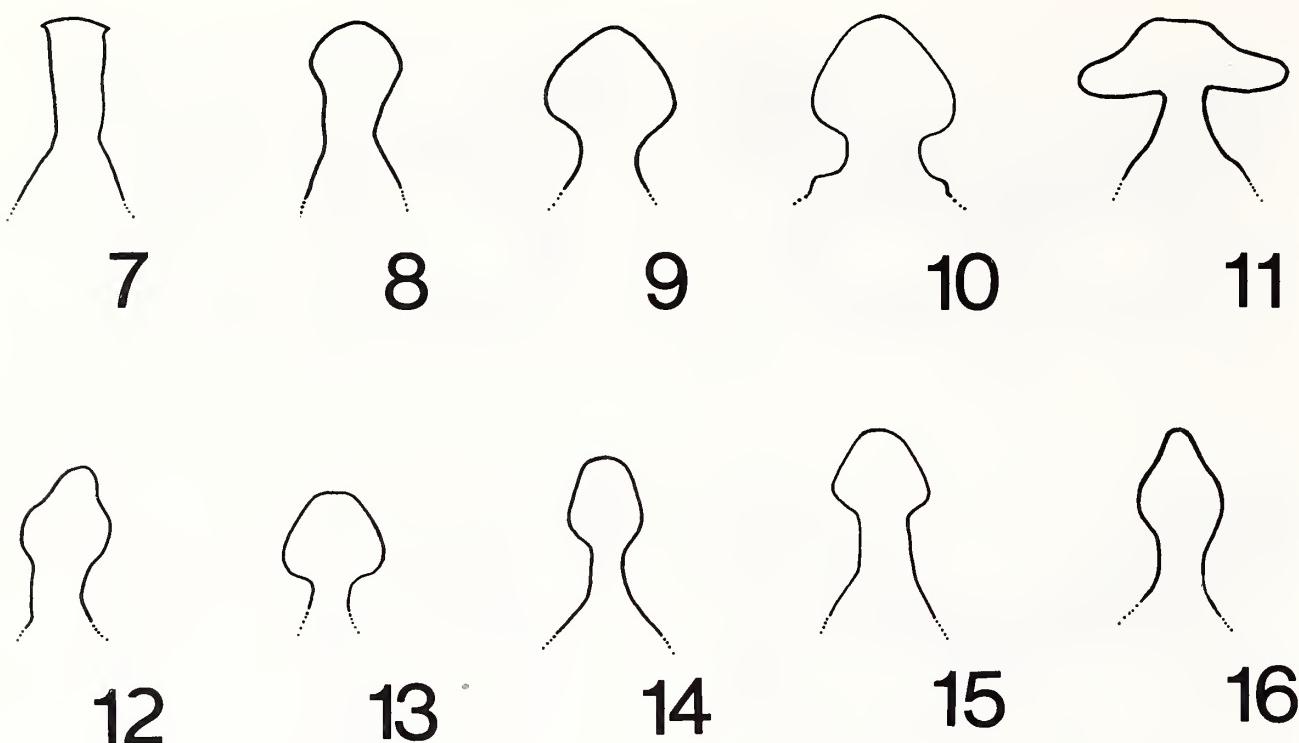


Figs. 1–6. Adults of *Aucula*, dorsal (left) and ventral views (right). 1–2. *A. franclemonti*, male; forewing length 25 mm; Ecuador, Carchi (CMNH). 3–4. *A. franclemonti*, female; forewing length 27 mm; Ecuador, Carchi (CMNH). 5–6. *A. franclemontoides*, holotype male; forewing length 24 mm; Ecuador, Morona-Santiago (CMNH).

variation not available to Todd and Poole. Eggs were also obtained and the immature stages reared; a larva was found feeding in the field and an adult female was reared from it, confirming the identity of the foodplant. The following paper reviews the systematics of *A. franclemonti* and closely related species, describes as new a related species from eastern Ecuador, describes the female genitalia, provides basic life history information, and presents a detailed morphological description of the larva in the context of other agaristine and noctuid larvae.

#### SYSTEMATICS OF THE *AUCULA FRANCLEMENTI* GROUP

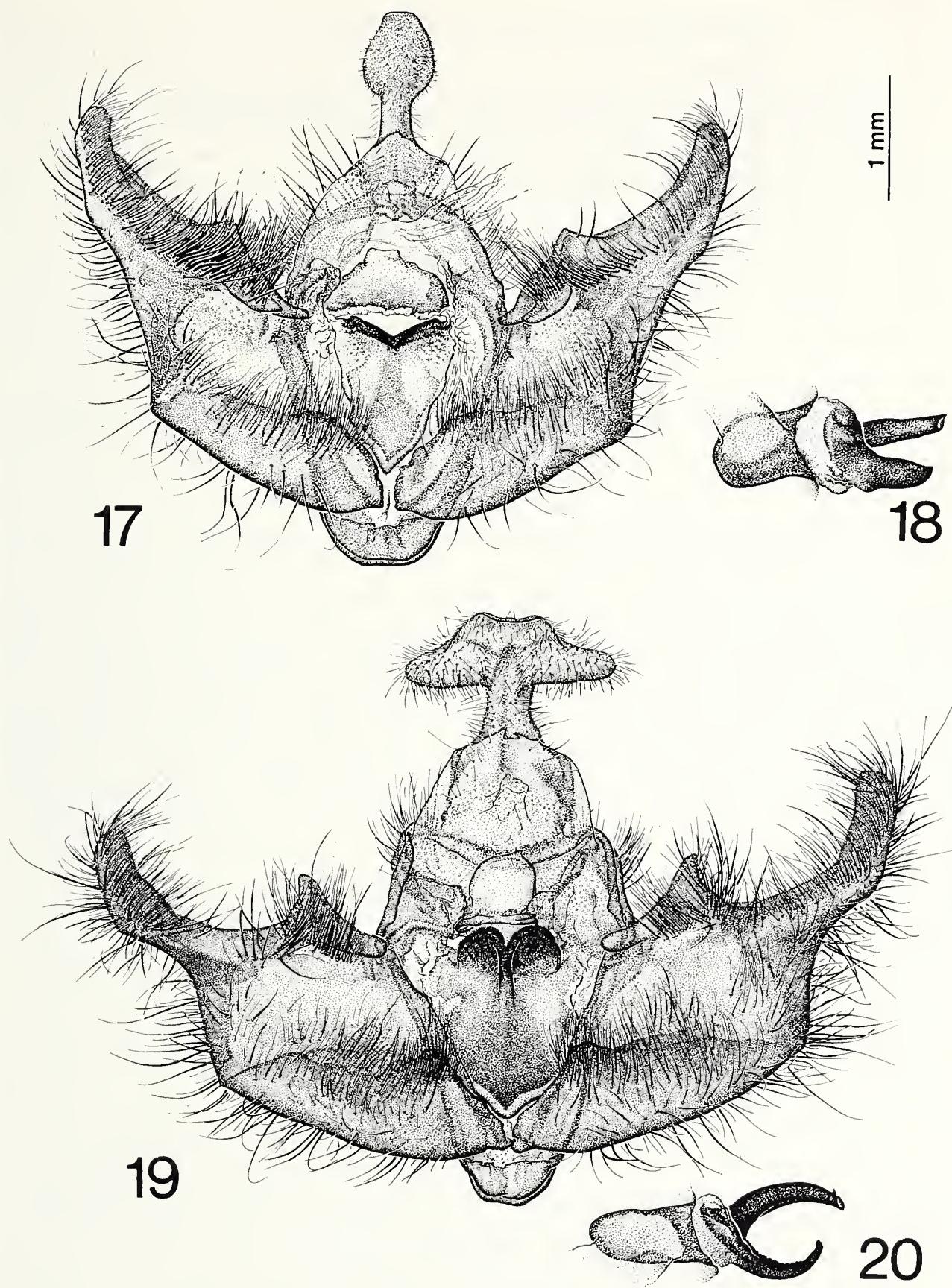
Todd and Poole (1981) informally recognized a group of six superficially identical species of *Aucula* from the Andes "characterized by an enlarged broad uncus and a



Figs. 7–16. Outlines of unci from male genitalia of species in the *Acula franclemonti* group (Figs. 7–10 and 12–13 taken from Todd and Poole (1981)). 7. *A. jenia*, holotype. 8. *A. otasa*, holotype. 9. *A. tusora*, holotype. 10. *A. ivia*, holotype. 11. *A. franclemontooides*, holotype (Genitalia slide: Rawlins 860 (CMNH)). 12. *A. kimsa*, holotype. 13. *A. franclemonti*, holotype. 14. *A. franclemonti* (Genitalia slide: Rawlins 849 (CMNH)). 15. *A. franclemonti* (Genitalia slide: Rawlins 858 (CMNH)). 16. *A. franclemonti* (Genitalia slide: Rawlins 857 (CMNH)).

characteristically shaped valve," the latter referring to the abruptly angled ventral margin at the distal end of the sacculus and a slender, setose, and smoothly arched valve apex. These genitalic features are unique to this group, both in the context of other species in the genus, as well as other species of Agaristinae (Kiriakoff, 1977). Their apomorphic condition supports the monophyly of a taxon here christened the *A. franclemonti* group. All specimens in this group examined by Todd and Poole were from Colombia and Ecuador west of the Andes, or from southern Peru and adjacent Bolivia east of the Andes.

Todd and Poole (1981) described the largest individuals in the group (FWL = 26–27 mm) as two species, *A. franclemonti* based on a single male (NMNH), and *A. kimsa* based on two males (BMNH). All type specimens of both species are from the same locality in western Colombia, San Antonio near Cali. The two species were distinguished by the shape of the distal half of the uncus, smoothly lobed in *A. franclemonti* (Fig. 13) and contrastingly concave in *A. kimsa* (Fig. 12). Similarly, Todd and Poole (1981) described two medium-sized species (FWL = 19–22) from northwestern Bolivia and adjacent southeastern Peru, *A. ivia* based on 18 males from both countries (NMNH, BMNH, CMNH), and *A. tusora* based on a single male from Bolivia. *A. tusora* was distinguished from *A. ivia* by the smoothly tapered base of the uncus, contrasting with a distinctive, angulate, or "shouldered" condition in *A. ivia*. Other than this condition, the habitus and male genitalia of the two species are virtually identical despite the somewhat worn condition of the unique type specimen of *A. tusora*.



Figs. 17–20. Male genitalia of *Aucula*. 17. External genitalia of *Aucula franclemonti* (Genitalia slide: Rawlins 848 (CMNH)). 18. Aedeagus of *Aucula franclemonti* (Genitalia slide: Rawlins 849 (CMNH)). 19. External genitalia of male holotype of *Aucula franclemontoides* (Genitalia slide: Rawlins 860 (CMNH)). 20. Aedeagus of male holotype of *Aucula franclemontoides*.

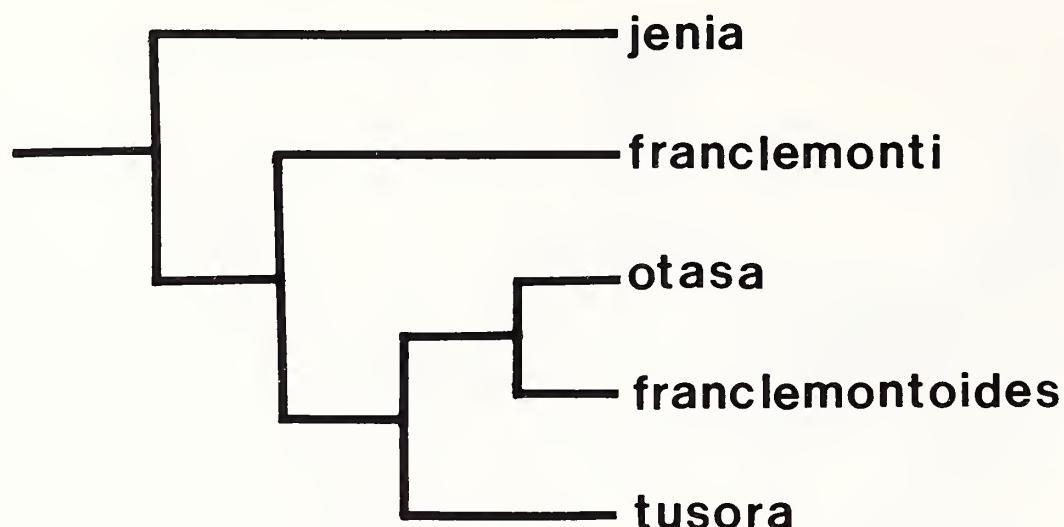


Fig. 21. Hypothesized phylogenetic relationship among species in the *Aucula franclemonti* species-group.

The *A. franclemonti* species-group contains two other distinctive and easily recognized species. The smallest in the group (length of forewing, FWL = 17 mm), *A. otasa* Todd and Poole, was described from a single Bolivian male (BMNH) and characterized by an autapomorphic incision of the dorsal margin of the sacculus, a very sharply angled emargination of the ventral outline of the valve apex distal to the saccular angulation, and a spatulate uncus (Fig. 8). Another medium-sized species from western Ecuador, *A. jenia* Todd and Poole (FWL = 23–24 mm), is easily recognized by an unique black bar across the yellow basal region on the ventral side of the hindwing (Fig. 25), and by male genitalia with a nearly straight outer margin beyond the saccular angulation and a broadened, strap-like uncus without lateral lobes (Fig. 7). The black wing bar is autapomorphic for *A. jenia*, but the genitalic features are considered plesiomorphic as for most species of *Aucula* other than those in the *A. franclemonti* group. One additional specimen of *A. jenia* has been examined and found to agree with all diagnostic features of the type series (Ecuador, Chimborazo, 11 km NE Pallatanga, 2,800 m, 11 November 1987, C. Young, R. Davidson, J. Rawlins (CMNH)).

Capture of 23 males in the *A. franclemonti* group at a single locality in northwestern Ecuador near the Colombian border (Ecuador, Carchi, Chical, 00°56'N, 78°11'W, 1,250 m, J. Rawlins, R. Davidson (CMNH)) provide new data on the nature and extent of variation in adult characters, including those purportedly diagnostic for *A. franclemonti* and *A. kimsa*. Specimens were taken during a period of intensive collecting extending from June 21 to August 16, 1983, and include the following dates (number of male specimens in parentheses): June 29 (1), July 1 (2), July 2 (6), July 5 (1), July 6 (1), July 8 (1), July 11 (3), July 15 (1), July 17 (4), July 18 (1), August 1 (1), August 7 (1). All genitalic features were assessed in six males by dissection, and the shape of the uncus and the distal half of the valve was examined in all remaining males by brushing abdominal apices.

All males were virtually identical in color and wing pattern (Figs. 1–2). There is slight variation in forewing size: FWL, 23–27 mm; mean = 24.8 mm; mode = 25 mm; N = 23. Several genitalic features are highly variable, especially the degree of setation and sclerotization of the valves and the shape and degree of sclerotization

of the uncus. In particular, the shape of the distal half of the uncus varies from a condition more deeply concave than that of the type specimen of *A. kimsa* to individuals with lateral lobes larger than those on the type specimen of *A. franclemonti* (Figs. 12–17). Collection of these specimens at a single locality over a short time period suggests they are conspecific members of a single population exhibiting considerable intrapopulation variation in genitalic characters, especially the shape of the uncus. Type specimens of *A. kimsa* and *A. franclemonti* fall within the range of character variation observed in this series, and their recognition as separate species is not supported. In contrast, some features of the male genitalia do not vary, notably the shape and sclerotization of the juxta, and the shape and size of the aedeagus (see discussion below).

The degree and extent of sclerotization at the base of the uncus in this conspecific series of *A. franclemonti* also varies greatly, ranging from a weakly sclerotized condition with smoothly arched outline to a more strongly sclerotized condition resulting in angled "shoulders" at the uncal base. The latter condition is very similar to the only diagnostic feature separating the single male type of *A. tusora* from the relatively extensive series of *A. ivia*, suggesting, albeit indirectly, that those two names represent but a single species as well.

In addition to the above specimens from western Ecuador, a single, slightly damaged specimen of *Aucula* was captured in Ecuador in a wet forest on the eastern slope of the Andes. Because this specimen was the first *Aucula* specimen known to me from the eastern Andean region north of southern Peru, special attention was given to its study. Externally the specimen closely resembles *A. franclemonti* and *A. tusora* (Fig. 3), but genitalic dissection revealed a distinctive new species of *Aucula* of the *A. franclemonti* group (Figs. 19–20).

#### *Aucula franclemontoides*, new species

Figs. 3–4, 19–20

**DIAGNOSIS.** This tropical American species is placed in the genus *Aucula* by the following combination of characters: rounded (not falcate) forewings, characteristic wing pattern (Fig. 3–4), lack of a yellow basal patch on the ventral side of the forewing, and male genitalia lacking a distinct median process on the sacculus. It differs from all described species of *Aucula* by features of the male genitalia, especially the strongly sclerotized, enlarged lobes on the dorsal margin of the juxta and the greatly enlarged and elongated lateral lobes of the uncus (Fig. 19).

**DESCRIPTION** (male only, female unknown). Forewing: length, 24 mm; maximum width, 12 mm. Hindwing: length, 18 mm. Extremely similar in all external features to *A. franclemonti* Todd and Poole, including antennal pectination, shape and size of frontal process, color pattern of wings and body; differs from *A. franclemonti* as follows: ground color of forewing brownish black, slightly darker and less reddish brown than *A. franclemonti* and similar in color to *A. jenia*; outer margin of yellow basal patch on hindwing smoothly and evenly curved as in *A. tusora* and *A. otasa*, not crenulate due to faint inward extension of black scales along veins as in *A. franclemonti* and *A. jenia*.

**Male abdomen.** Abdominal terga 3–7 with antecostae evanescent on midline; Ter-

gum 8 subquadrate, unmodified; Sternum 8 with anterior margin slightly thickened and sinuate. Abdominal Segment 2 with lateral hair pencils resting in scale-lined, elongate pleural invaginations on segments 2–4.

*Male genitalia.* Figures 19–20. Tegumen slightly wider than long, strongly sclerotized dorsally, membranous ventrally. Vinculum narrow; saccus not developed. Juxta a smooth flattened plate, subacute ventrally, prolonged dorsally into two rounded and posteriorly extended lobes separated by a deep notch; lobes of juxta heavily sclerotized, densely covered with microscopic spinules. Anellifer membranous except in region immediately adjacent to aedeagus. Uncus inflated at base to more than half width of tegumen, narrowly constricted at middle, then abruptly dilated into two long lateral lobes and terminated in a very short, broadly truncated, and slightly asymmetrical apex. Valves symmetrical, subtrapezoidal, with elongate, curved apices; costa with large triangular process at middle subtended by flat, coarsely setose editum; sacculus broad, setose, with ventral margin smoothly curved, forming abrupt obtuse angle with apex of valve; dorsal margin of sacculus distinct, raised into rounded prominence near base of valve; apex of valve constricted distally with outline strongly concave ventrally and dorsally; valve with distal end slightly flattened and widened, dorsally deflected, and densely setose on mesal surface.

Aedeagus greatly modified (Fig. 20); basiphallus broadly expanded anteriorly into a weakly sclerotized coecum; distiphallus shorter than its diameter, but bearing dorsally a strongly sclerotized, flattened, apical process which curves smoothly ventrad; endophallus (vesica) permanently everted, very heavily sclerotized, forming a hollow tube curved dorsad, terminated in a subcircular meatus (primary gonopore) with a minute spinule approximate to its ventral lip.

**BIOLOGY AND IMMATURE STAGES.** Unknown, but are expected to be very similar to those of *A. franclemonti*, described below. Expected foodplants for *A. franclemontoides* and other species of *Aucula* are species of *Vitis* and related genera of Vitaceae.

**DISTRIBUTION.** Known only from the type locality where the habitat is submontane rainforest of exceptional richness and floristic diversity.

**DISCUSSION.** Diagnostic modifications of the juxta and uncus leave little doubt that this species is distinct from other members of the *A. franclemonti* group.

Of special interest is the aedeagus, which is similar to those of other species in the *A. franclemonti* group, none of which was figured by Todd and Poole (1981). They interpreted the aedeagus to have a “vesica without spines or cornuti,” but careful study and dismemberment of one aedeagus did not reveal any eversible structure beyond the external meatus of the strongly sclerotized, tubelike apex of the phallus. Comparative study of the aedeagus reveals that the basiphallus (portion of aedeagus internal to junction with anellus (manica)) is inflated and weakly sclerotized. The distiphallus (sclerotized external portion of aedeagus from manica to base of endophallus) is very short with an elongate dorsal process. The endophallus is not membranous, but rather very strongly sclerotized into a permanently everted tube so that the apparent apical opening of the phallus is the primary gonopore, not the secondary gonopore (phallotreme) as is the usual case in most Lepidoptera.

**PRIMARY TYPE DATA.** Holotype male, CMNH. Verbatim text of four pin labels: ECUADOR: Morona-Santiago. Rio Culebrillas, 34 km SE Gualaceo. 2,200 m. 22–23 Oct 1987 / J. Rawlins, C. Young, R. Davidson. Wet forest. / Genitalia

Slide No. 860 John E. Rawlins / HOLOTYPE *Aucula franclemontoides* Rawlins [red paper].

*Etymology:* The name *franclemontoides* is an adjective referring to the great resemblance of this species to *A. franclemonti*.

#### ALPHABETICAL CHECKLIST OF SPECIES IN THE *AUCULA FRANCLEMONTI* GROUP

*Aucula franclemonti* Todd and Poole, 1981.

*Aucula kimsa* Todd and Poole, 1981. **NEW SYNONYMY.**

*Aucula franclemontoides* Rawlins, new species.

*Aucula jenia* Todd and Poole, 1981.

*Aucula otasa* Todd and Poole, 1981.

*Aucula tusora* Todd and Poole, 1981.

*Aucula ivia* Todd and Poole, 1981. **NEW SYNONYMY.**

#### KEY TO ADULTS OF SPECIES IN THE *AUCULA FRANCLEMONTI* GROUP

BASED PRIMARILY ON THE MALE GENITALIA

(Derived in part from key in Todd and Poole, 1981)

1. Uncus widest near middle (Figs. 8–17, 19); yellow region on lower surface of HW unmarked (Figs. 2, 4, 6) ..... 2
- Uncus widest at apex, strap-like (Fig. 7); yellow region on lower surface of HW with black stripe across middle (Fig. 25) ..... *jenia*
2. Dorsal margin of sacculus with triangular lobe near middle; apical part of valve nearly straight ..... *otasa*
- Dorsal margin of sacculus not lobed; apical part of valve distinctly curved ..... 3
3. Sclerotized dorsal edge of juxta v-shaped, the convergent sides nearly straight in outline (Fig. 17); uncus with lateral outline slightly concave, straight, or evenly convex (Figs. 12–17) ..... *franclemonti*
- Sclerotized dorsal edge of juxta with two rounded lobes protruded posteriorly, in outline forming two rounded lips separated by a distinct notch (Fig. 19); uncus with lateral lobes ..... 4
4. Uncus with distal lateral outline evenly convex (similar to Figs. 9–10) ..... *tusora*
- Uncus with greatly enlarged lateral lobes (Figs. 11, 19) ..... *franclemontoides*, n. sp.

#### PHYLOGENETIC RELATIONSHIPS

There are few characters shared among the five species of the *A. franclemonti* group that permit phylogenetic analysis relative to an outgroup consisting of all other species of *Aucula*. Five informative characters were observed as follows, the state occurring in the outgroup scored 0:

*Character 1.* Lateral lobes of uncus: 0, present; 1, absent.

*Character 2.* Lateroventral outline of apical half of valve: 0, straight; 1, concave, smoothly curved; 2, concave, deeply angled.

*Character 3.* Distinct, rounded lobes on dorsal edge of juxta: 0, absent; 1, present.

*Character 4.* Ventral outline of valve at distal end of sacculus: 0, smoothly curved; 1, sharply angled.

*Character 5.* Length of free, apical extension of valve: 0, apex of valve not conspicuously elongated; 1, apex of valve elongated and constricted.

Characters were distributed as follows, with the number of each character followed by its state in parentheses: *A. jenia*, 1(0), 2(0), 3(0), 4(1), 5(1); *A. otasa*, 1(1), 2(2), 3(1), 4(1), 5(1); *A. franclemonti*, 1(1), 2(1), 3(0), 4(1), 5(1); *A. franclemontoides*, 1(1), 2(2), 3(1), 4(1), 5(1); *A. tusora*, 1(1), 2(1), 3(1), 4(1), 5(1); other *Aucula* species (outgroup), 1(0), 2(0), 3(0), 4(0), 5(0). Characters autapomorphic for single species were not considered, such as small body size and a notch in the dorsal margin of sacculus in *A. otasa*, the black HW stripe in *A. jenia*, huge uncal lobes in *A. franclemontoides*, and a relatively short apical elongation of the valve in *A. tusora*.

A phylogenetic analysis produced a minimally supported but fully resolved hypothesis of relationship. All possible phylogenetic trees (105) were examined with respect to the above five characters, and a single tree of minimum length (Fig. 21) was found without invoking hypotheses of homoplasy (Consistency = 1.00). East Andean species from Ecuador, Peru, and Bolivia (*A. tusora*, *A. otasa*, and *A. franclemontoides*) are hypothesized to form a monophyletic subgroup based on distinctive lobing of the *juxta*. This subgroup and *A. franclemonti* form a monophyletic group supported by two synapomorphies, uncal lobes and an inwardly curved or angled ventral margin along the outer half of the valve.

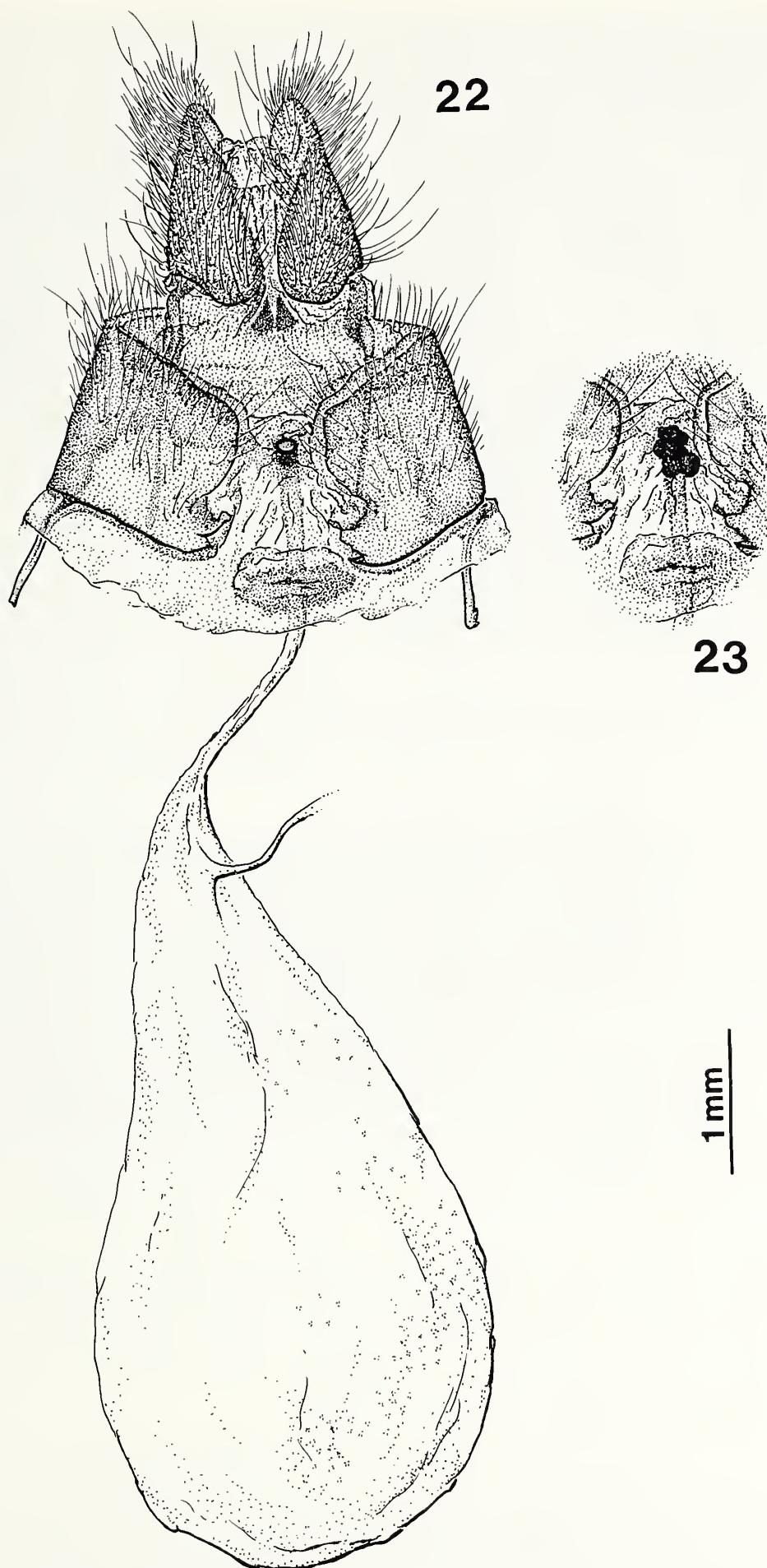
The monophyly of the *A. franclemonti* group is supported by two derived characters, apical elongation of the valves and a sharply angled ventral margin at the distal end of the sacculus. On the other hand, there is no evidence that other species of *Aucula* form a monophyletic group, and genitalic features suggest that the immediate sister-lineage to the *A. franclemonti* group may be one including *Aucula byla* Todd and Poole. There is also serious question whether the genus *Aucula* is monophyletic as treated by Todd and Poole (1981), because diagnostic features currently used to define the genus, such as wing shape, coloration, and the absence of a median process of the sacculus, are not convincingly apomorphic at the level of Agaristinae.

#### DESCRIPTION OF THE ADULT FEMALE OF *AUCULA FRANCLEMONTI*

Todd and Poole only briefly described females of *Aucula* and their genitalia. A more complete description of female *A. franclemonti* is given here based on three specimens, two mated females caught in the field (one is the female parent of CMNH Culture 83-186), and a single virgin female eclosing in the laboratory (CMNH Culture 83-351).

*General.* Maculation, color, and shape as in males with the following differences: size slightly larger than males (FWL = 27–28 mm); costa of forewing slightly but distinctly angled just beyond middle; apical segment of labial palp more than twice as long as wide (length and width subequal in males).

*Female genitalia.* Figure 22. Lobes of papillae anales subtriangular due to slight elongation of posterior dorsal angle; lobes sparsely setose, more densely so near posterior margins; posterior apophyses compressed and widened near base, cylindrical anteriorly, subequal in length to papillae anales; Tergum 8 unmodified; anterior apophyses slightly shorter than posterior apophyses; ostium bursae small, circular, sclerotized, located in membranous protuberance between ventral edges of Tergum 8; ductus bursae straight, slender, membranous, sclerotized only at extreme base by ostium bursae; corpus bursae membranous, ovoid, tapered smoothly into ductus bursae; anterior enlargement of corpus bursae (fundus bursae) without signa but with



Figs. 22–23. Female genitalia of *Aucula franclementi* (Genitalia slide: Rawlins 859 (CMNH)).  
22. Ventral view without sphragis. 23. Detail of ostial region with sphragis in position.



25

Figs. 24–25. Ventral view of *Aucula* species. 24. Female of *A. franclemonti* (CMNH Culture No. 83-351) during reflex immobilization following a slight disturbance. 25. Ventral view of *A. jenia*, male; forewing length 23 mm; Ecuador, Chimborazo (CMNH).

sparingly scattered acanthalae; small medial zone of irregular sclerotization anterior to ostium bursae, reflexed under Sternum 7; posterior margin of Sternum 7 sclerotized, broadly concave. Mated female without discernable internal spermatophore; plug of amorphous sclerotized material in ostium bursae (Fig. 23), extended inward along short sclerotized base of ductus bursae, and outward over protuberance encircling ostium.

*Discussion.* The external female genitalia are structurally correlated in size and shape with the male genitalia. The small ostium and adjacent sclerotized portion of the ductus bursae match precisely in diameter and length the permanently everted and strongly sclerotized endophalli of males.

A sclerotized plug was present in the ostia bursarum of both mated females, and absent in the single female known to be virgin by virtue of its having eclosed in isolation. The chitinous nature of this copulatory obstruction suggests that it is probably homologous to the collum of the unmodified noctuid spermatophore. Its presence in both mated females available for study, and its absence in a virgin female, suggests that it is functioning as a sphragis preventing multiple matings. I am not aware of sphragides elsewhere in the Noctuidae.

#### LIFE HISTORY NOTES ON *AUCULA FRANCLEMONTI*

A female of *A. franclemonti* was collected on 5 July 1983 at the same Ecuadorian locality as the series of 23 males discussed above. A search was made for likely foodplants in the Onagraceae, Vitaceae, and Portulacaceae in anticipation of obtaining another gravid female. Another female was taken on the night of July 11. When



Figs. 26-27. Immature stages of *Aucula franclemonti* (CMNH Culture No. 83-351). 26. Last larval instar resting on under surface of leaves of foodplant, *Vitis tiliifolia*. 27. Pupa exposed in pupal chamber formed by boring in soft wood; pupal position reversed from that found in nature.

placed in a small container with leaves of a wild grape (*Vitis*, Vitaceae), it deposited 28 eggs by the morning of July 12. These hatched after an incubation period of slightly more than four days. Five eggs and five first instars were preserved (CMNH Culture 83-186), and the remaining larvae began feeding at once on the dorsal surface of wild grape leaves. First instar larvae remained relatively immobile on the leaves while feeding, but when disturbed moved about rapidly as "semiloopers" with prolegs advancing the length of two or more segments at each step (multisegmental loco-

motion). Detailed developmental observations were not made, but three late third instars were preserved on July 26, and two last larval instars (fifth) were preserved on August 3, 18 days after hatching. The last three instars moved by advancing the prolegs a single segment per step without semilooping (unisegmental locomotion), and fed by biting leaf edges.

During the rapid development of this isofemale culture, larvae were sought in the field on foliage of the same species of *Vitis*. During the night of 26 July 1983, a last instar larva was found feeding by Mark Smyers (Fig. 26). On July 31, the larva began boring into rotting wood, constructing a pupation chamber which was rendered observable by carefully splitting the piece of wood into which it had bored. The chamber was completed by August 1, and the prepupa remained inactive for four days, pupating on August 5 (Fig. 27). The pupal chamber was transported back to a laboratory at the University of Texas, Austin. By rare good fortune, eclosion of a female moth was directly observed on 11 September 1983 at 10:00 hours CST. The freshly eclosed moth climbed up to an elevated position in the laboratory enclosure and remained motionless for nearly 40 minutes before expansion of the wings. When disturbed, this virgin female defended itself by reflex immobilization with the wings appressed stiffly above the abdomen and the abdomen expanded and strongly curved under the thorax (Fig. 24), similar to the behavior of wild-caught males and other aposematic Lepidoptera, including a diversity of sympatric Arctiidae (Watson, 1975).

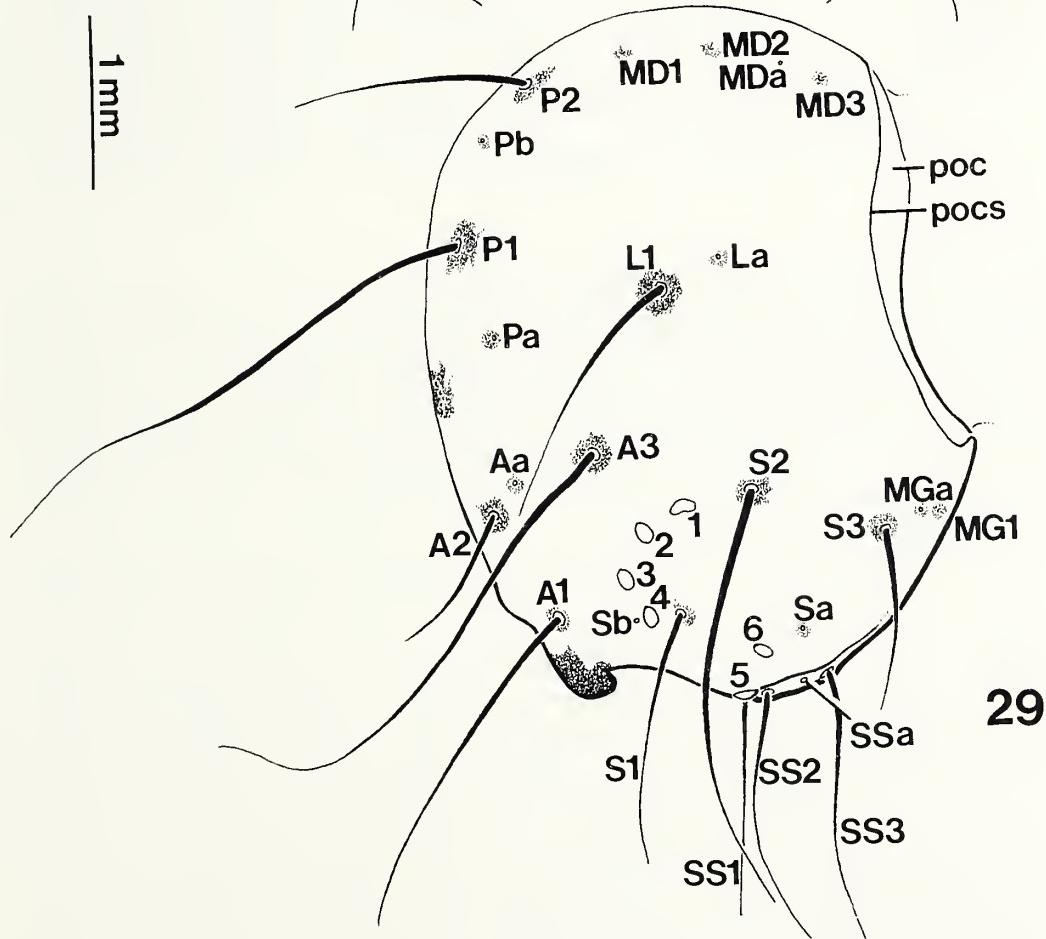
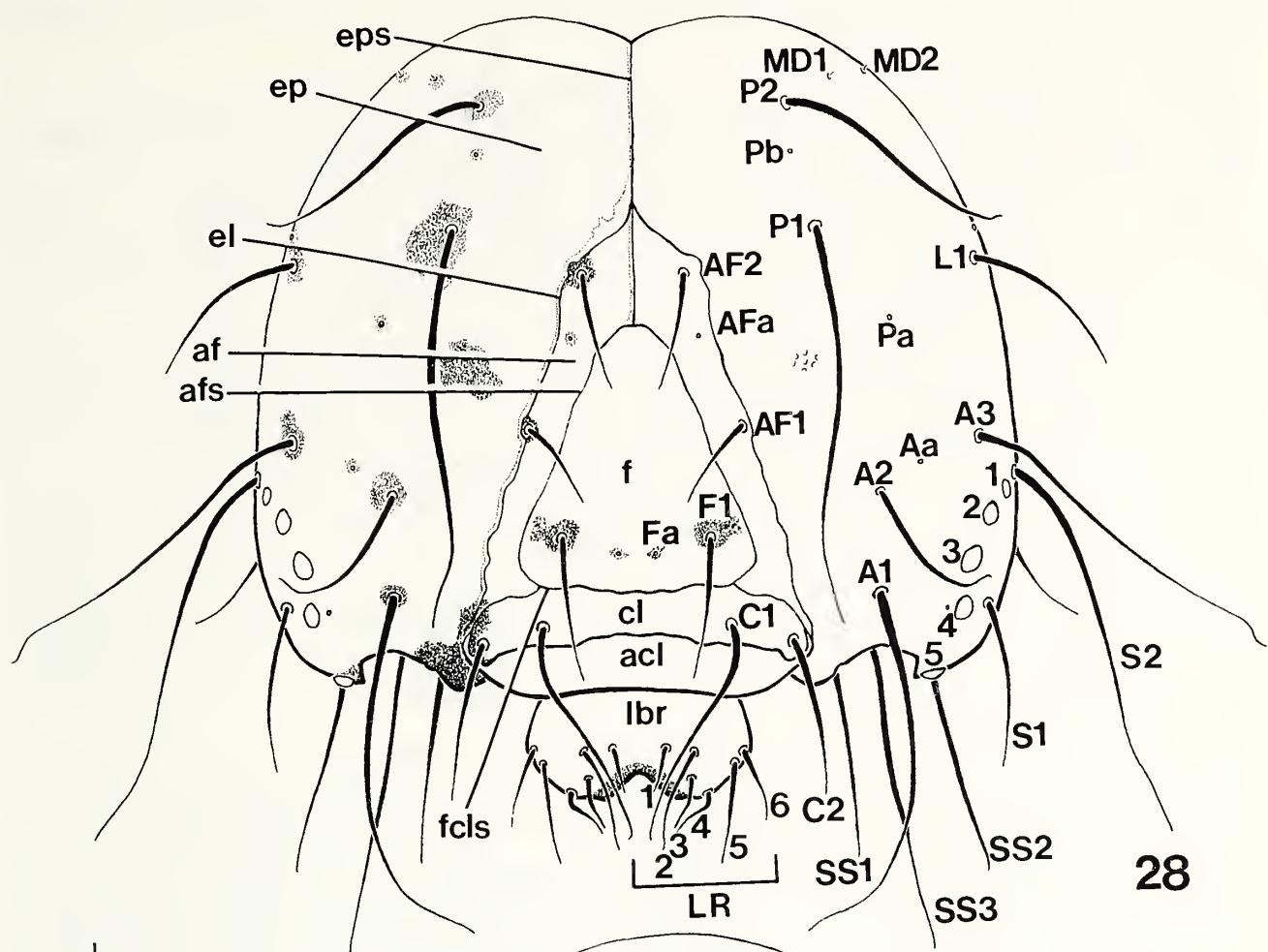
*Foodplant:* *Vitis tiliifolia* Humb. & Bonpl. ex. Roem. & Schultes; voucher specimen in herbarium of Carnegie Museum, Thompson and Rawlins No. 811, collected 10 July 1983. Determination by Michael O. Moore, 1990, The University of Georgia.

The immature stages of *A. franclemonti* are described briefly below.

*Egg:* Deposited singly or in clumps of 2–3 against major veins on underside of leaf of foodplant, partially or completely inserted under lanate pubescence. Pale yellow when laid, turning reddish brown prior to hatch. Egg slightly variable in size and shape, moderately flattened; diameter, 0.96–1.09 mm; height, 0.60–0.74 mm. Microsculpture consisting of 22–25 vertical costulae only slightly raised above outline of egg; all vertical costulae begin near outer edge of flattened base of egg, but only half extend to micropylar rosette, the other half evanescing at about  $\frac{1}{8}$  the distance to rosette; long and short vertical costulae alternating; vertical costulae connected by diffuse transverse costulae, separating columns of 10–13 indistinct areoles. Micro-



Figs. 28–29. Chaetotaxy of the head of last instar larva of *Aucula franclemonti*. 28. Dorsofrontal view of head. 29. Lateral view of head. Symbols used: A1–A3, anterior setae; Aa, anterior pore; acl, anteclypeus; af, adfrontal sclerite; AF1–AF2, adfrontal setae; AFa, adfrontal pore; afs, adfrontal suture (=lateral adfrontal suture); cl, clypeus (=postclypeus of authors); CL1–CL2, clypeal setae; el, ecdysial line; ep, epicranium; eps, epicranial suture (=coronal suture or medial adfrontal suture); f, front; F1, frontal seta; Fa, frontal pore; fcls, frontoclypeal suture; L1, lateral seta; La, lateral pore; lbr, labrum; LR1–LR6, labral setae; MD1–MD3, dorsal proprioceptor setae; MDa, dorsal pore; MG1, genal proprioceptor seta; MGa, genal pore; P1–P2, posterior setae; Pa–Pb, posterior pores of head; poc, postocciput; pocs, postoccipital suture; S1–S3, stemmatal setae; Sa–Sb, posterior stemmatal pores; SS1–SS3, substemmatal setae; SSA, substemmatal pore.



pylar rosette less than 0.10 mm in diameter, surrounded by a slight depression joining upper ends of vertical costulae.

*First instar:* Length, 2.8–3.2 mm; width of head, 0.52 mm. Head yellowish brown, body pale grayish white with long white setae arising from contrasting brown pinaculae. Tactile setae as in last instar with the following exceptions: only one SV seta present on A1 and A7, two SV setae present on A2; five coxal setae (DC1–DC2 missing, Figs. 36–37). Prolegs on A5 and A6 subequal, those on A4 slightly smaller, those on A3 still smaller.

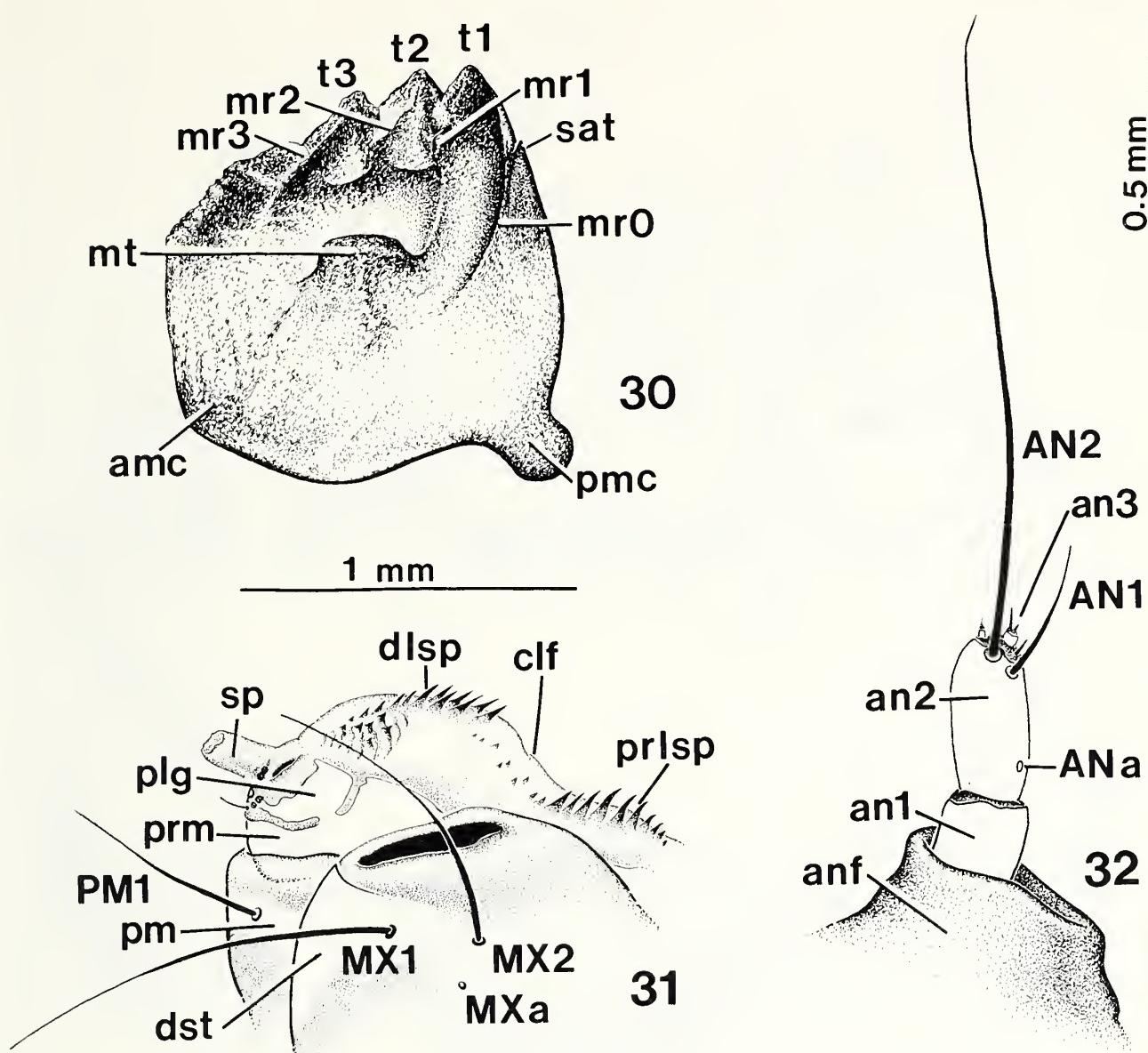
*Intermediate instars:* Head yellow, with setal bases minutely but contrastingly dark brown. Body color pale reddish gray, densely spotted with dark spots vaguely forming broken transverse stripes. Two SV setae on A7, the anteriormost seta (SV2) much smaller than the posterior and on a separate pinaculum.

*Last instar:* Length, 48 mm; head width, 4.5 mm; width of mandible, 1.16 mm. Head blocky, strongly hypognathous, width greater than prothorax. Body elongate, enlarged gradually posteriorly, distinctly swollen on Ab8; most setae long, conspicuous, erect (especially on segment Ab8), set in distinct, slightly elevated pinaculae which are enlarged dorsally (especially dorsal pinaculae on segment Ab8). Detailed chaetotaxy and external morphology presented below.

Head pale brownish yellow, bases of setae brownish black. Thorax and abdomen with ground color light gray tinted with olivaceous to yellowish brown on middle of segments; pattern of dark gray to black spots, forming irregular transverse bands on posterior portion of segments; transverse pattern less distinct anteriorly on each segment; segments T2 to Ab9 with large blotches of white laterally, most extensive on sides of Ab7 in subdorsal and lateral regions; ventral region on all segments pale yellowish white, contrasting with adjacent subventral color. Prothoracic and anal shields concolorous with head; thoracic legs brownish yellow on ventral and lateral surfaces, darker brown on dorsal surface; subventral pinaculum above prolegs yellowish brown dorsally, darker brown ventrally; spiracles black; most setae pale gray to white.

*Pupa* (terminology follows Mosher, 1916): Length, 22 mm. Pupa very dark reddish brown, dull in lustre due to strong microsculpture which is finely spinulose dorsally. Labial palpus visible externally; base of maxilla extended laterally to sculptured eyepiece; prothoracic femur not visible; mesothoracic leg not extended anteriorly to sculptured eyepiece (externally not contiguous with eyepiece); terga 3 and 4 separated by flexible cuticle, not fused; cremaster truncate, with flattened lateral processes bearing reduced setae along posterior margins.

*Discussion:* Although the egg does not differ in a distinctive way from many other non-agaristine noctuids, the larval and pupal stages of *A. franclemonti* are characteristic of those found in a diverse representation of other agaristines that I have reared and studied in detail (e.g., *Alypia octomaculata* (Fabricius), *Brephos nyassana* (Bartel), *Chelonomorpha formosana* Miyake, *Euscirrhopterus gloveri* Grote and Robinson, *Eudryas grata* (Fabricius), *Eudryas unio* (Hübner), *Mimeusemia vilemani* Hampson, *Psychomorpha epimenis* (Drury), *Tuerta chrysochlora* Walker, *Xerociris wilsonii* (Grote)). In particular, mature larvae are characterized by pale, hypognathous head capsules with setal insertions often accentuated with dark spots; body segments with contrasting transverse patterns of 1–8 bands, sometimes broken into spots (*Aucula*) or obscured by a dark ground (*Xerociris*), often with patches of orange or white laterally. These larval generalizations hold for many species described in some



Figs. 30–32. Mouthparts of last instar larva of *Aucula franclementi*. 30. Medial surface of left mandible. 31. Left lateral view of hypopharyngeal complex, labial and maxillary palp; removed. 32. Left antenna. Symbols used: amc, anterior mandibular condyle; AN1–AN2, setae of an2; an1–an3, antennal segments; ANa, pore of an2; anf, antennifer; clf, transverse cleft of hypopharynx; dlsp, distolateral spinules; dst, dististipes (=palpifer of authors); mr0, outer mandibular ridge; mr1–mr3, inner mandibular ridges; mt, inner tooth; MX1–MX2, setae of maxillary stipes; MXa, pore of basistipes; plg, palpiger (=stipes labii of Crumb (1929)); pm, postmentum; PM1, postmental seta; pmc, posterior mandibular condyle; prlsp, proximolateral spinules; prm, prementum; sat, subapical cleft; t1–t3, apical teeth.

detail by Gardner (1946, 1948; *Aegocera venulia* (Cramer), *Sarbanissa albifascia* (Walker)), by Crumb (1956; *Alypia langtonii* Couper, *Alypia ridingsii* Grote, *Androloma maccullochii* (Kirby) (but body pattern longitudinal), *Eudryas brevipennis* Stretch, *Euscirrhopterus cosyra* (Druce)), those figured by Sugi (1987; *Asteropetes noctuina* (Butler), *Chelonomorpha japonica* Motschulsky, *Maikona jezoensis* Matsumura, *Sarbanissa subflava* (Moore), *S. venusta* (Leech)) and those figured by Common (1990; *Agarista agricola* (Donovan), *Argyrolepidia subaspersa* (Walker), *Cruria donowani* (Boisduval), *Comocrus behri* (Angas), *Periscepta polysticta* (Butler), *Phalaenoides tristifica* (Hübner)). Of all agaristines known to this author, the immature stages of *A. franclementi* most closely resemble those of *Mimeusemia vilemani* from Taiwan.

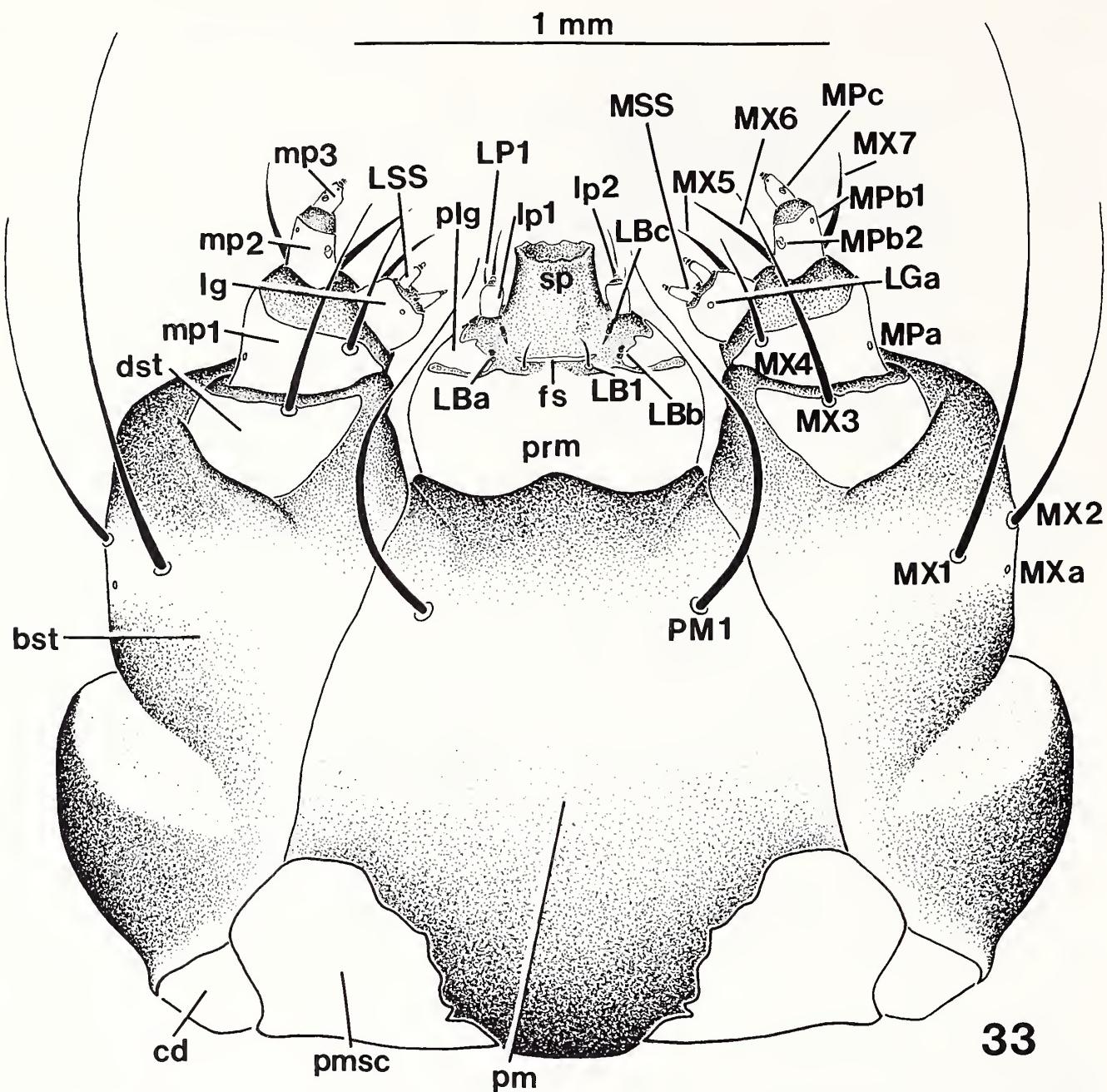
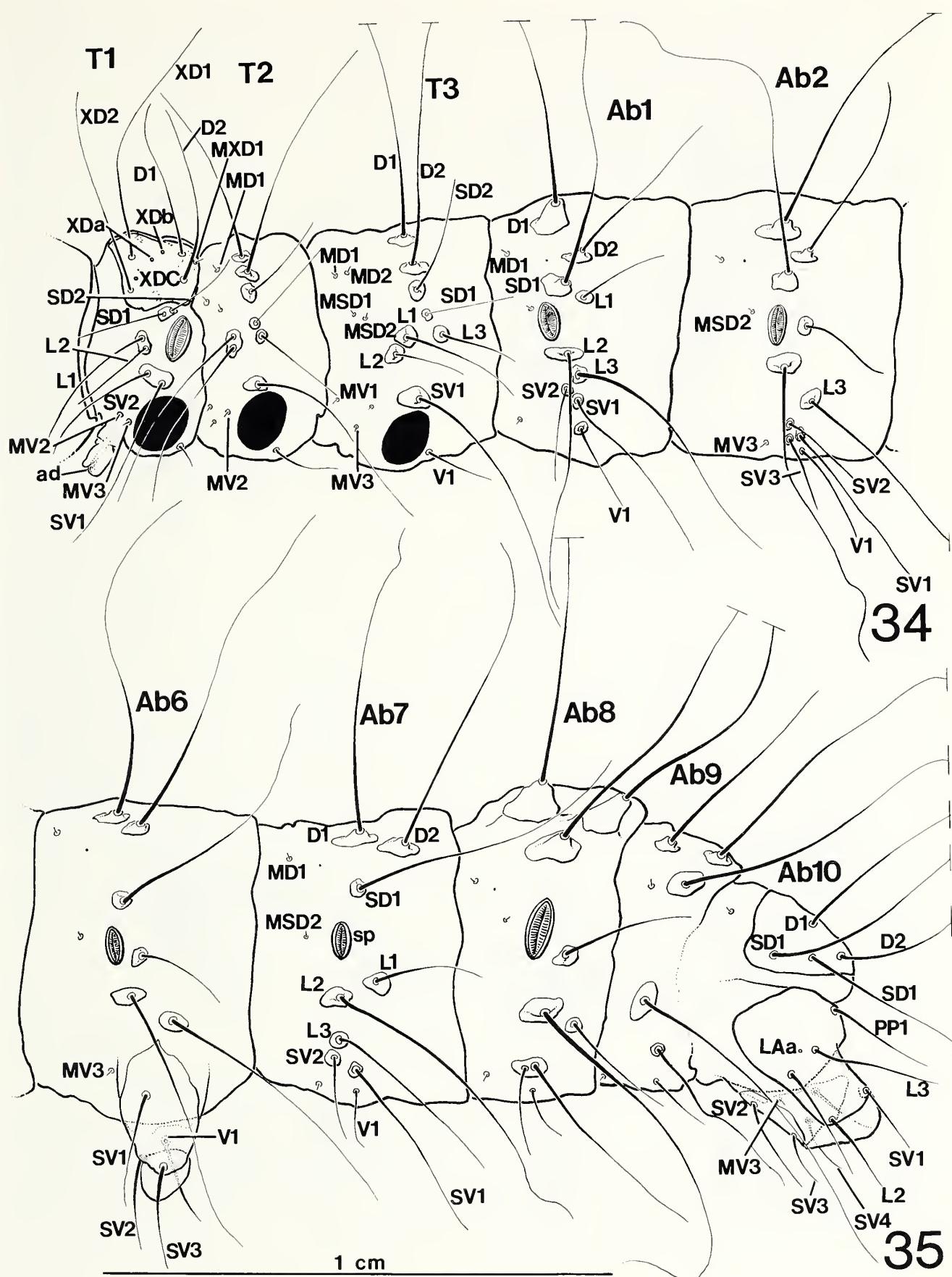
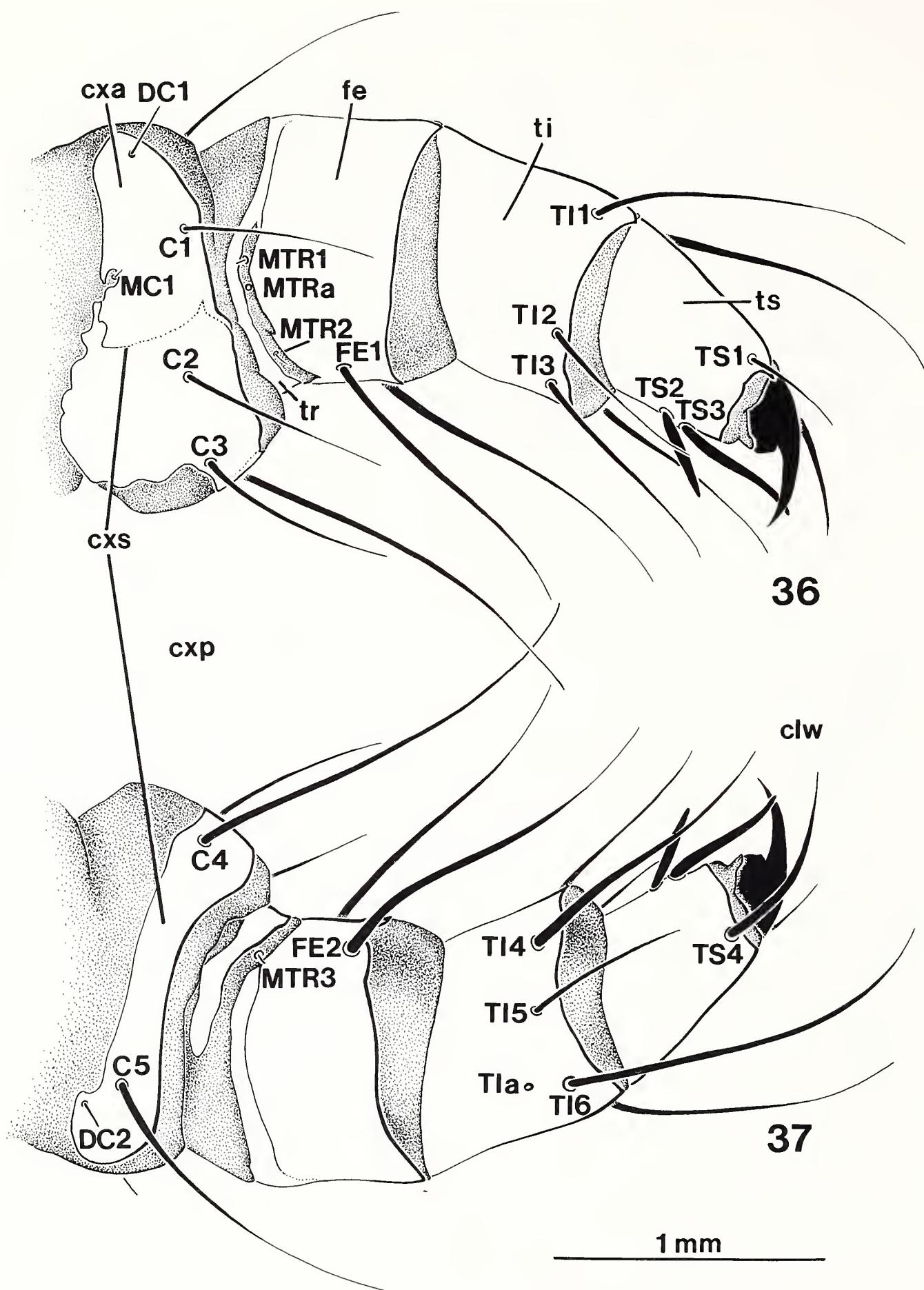


Fig. 33. Maxillolabial complex of last instar larva of *Aucula franclemonti* (semischematic). Symbols used: bst, basistipes; cd, cardo; dst, dististipes; fs, fusiliger; LB1, stipular seta of labium; LBa–LBc, pores of palpiger; lg, laciiniogalea; LGa, pore of laciiniogalea (=Mxe of Gerasimov); LP1, apical seta of lp1; lp1, basal segment of labial palpus; lp2, distal segment of labial palpus; LSS, lateral sensillum styloconicum of laciiniogalea; mp1–mp3, segments of maxillary palpus; MPa, pore of basal segment of maxillary palpus (=Mxd of Gerasimov); MPb1, lateral pore of mp2 (=Mxf of Gerasimov); MPb2, medial sensillum of mp2; MPC, pore of mp3 (=Mxj of Gerasimov (1952)); =SD of Grimes and Neunzig (1986a); MSS, medial sensillum styloconicum of laciiniogalea; MX1–MX3, setae of maxillary stipes; MX4, seta of first segment of maxillary palpus; MX5–MX7, apical setae of maxilla (=STIII-STI of Grimes and Neunzig, 1986b)); MXa, pore of basistipes; plg, palpiger; pm, postmentum; PM1, postmental seta; pmSC, posterior sclerotization of postmentum; prm, prementum; sp, spinneret.

→  
 Figs. 34–35. Chaetotaxy of the body segments of last larval instar of *Aucula franclemonti* (semischematic views). 34. Left side of thorax and first two abdominal segments. 35. Left side of abdominal segments 6–10. Symbols used (broken outlines indicate features hidden from view by other structures): Ab1–Ab10, abdominal segments; ad, adenosma (ventral cervical



gland); D1–D2, dorsal setae; L1–L3, lateral setae; LAa, lateral pore of Ab10; MD1, dorsal proprioceptor seta; MSD1–MSD2, subdorsal proprioceptor setae; MV1–MV3, ventral proprioceptor setae; MXD1, posterior proprioceptor seta of T1; PP1, paraproct seta; SD1–SD2, subdorsal setae; spr, spiracle; SV1–SV4, subventral setae; T1–T3, thoracic segments; V1, ventral seta; XD1–XD2, anterior dorsal setae of T1; XDa–XDC, anterodorsal pores of T1.



Figs. 36–37. Chaetotaxy of the prothoracic leg of last instar larva of *Acula franclemonti*. 36. Anterior view of left prothoracic leg. 37. Posterior view of left prothoracic leg. Symbols used: C1, seta of anterior coxal sclerite; C2–C5, setae of posterior coxal sclerite; clw, claw of pretarsus; cxa, anterior sclerite of coxa; cxp, posterior sclerite of coxa; cxs, coxal suture; DC1–

The pupation chamber and pupa of *A. franclemonti* are also very similar to those of agaristine species I have studied (see list above). Pupation occurs in chambers bored in soft wood. Pupae characteristically have heavy microsculpture, are often spinulose dorsally, and the truncate cremaster bears flattened lateral flanges with setae greatly reduced or absent. The labial palpi are visible, the prothoracic femora are not, and the mesothoracic leg is not contiguous with the eyepiece. Terga 3 and 4 are not fused but are closely joined by flexible intersegmental cuticle.

The vitaceous host of *A. franclemonti* is expected, as most of the known foodplants for agaristine species worldwide are in the Vitaceae, including Leeaceae (Rhamnales), and the remainder in the following unrelated families of plants: Dilleniaceae (Dilleniales); Lauraceae (Laurales); Onagraceae (Myrtales); Haloragaceae (Haloragales); Portulacaceae, Nyctaginaceae and Cactaceae (Caryophyllales); Loranthaceae (Santalales); Boraginaceae (Lamiales); Rubiaceae (Rubiiales); Araceae (Arales); Smilacaceae and Dioscoreaceae (Liliales).

#### CHAETOTAXY OF THE MATURE LARVA OF *AUCULA FRANCLEMONTI*

Chaetotaxy and general morphological features are presented in considerable detail in Figure 28–37. No previous author has presented exhaustively the chaetotaxy of an entire larval noctuid, although a consistently applied terminology for most setae has emerged in recent years as best summarized by Stehr (1987). Current setal nomenclature for Lepidoptera larvae results from a long and confusing history of comparative study including Fracker (1915), Schierbeek (1917), Hinton (1946), Gerasimov (1952), and Hasenfuss (1963). Descriptive work with noctuid larvae has become increasingly refined since early work by Ripley (1923) and Crumb (1929), through comprehensive, regional treatments by Gardner (1946, 1948), Crumb (1956), Beck (1960), and Godfrey (1972, 1987), to an exceptionally detailed and well-illustrated work by Miller (1991) who illustrated the partial chaetotaxy of the agaristine *Alypia octomaculata*. Beck (1960) and Godfrey (1972) provide nomenclature for the hypopharyngeal complex, and Godfrey (1972) supplies a general rationale for description of the mandible, similar in principle to that proposed by Gerasimov (1952). A review of chaetotaxy for abdominal segment 10 was given by Stehr (1987), but locations for the various setae were not clearly illustrated and application of his terminology remains problematic for lateral and subventral setae of the last abdominal segment.

Two systems, the maxillolabial complex and the thoracic legs, have not been consistently illustrated or labelled in larval descriptions, although Gerasimov (1952) offered a system naming most setae. Grimes and Neunzig (1986a, 1986b) provided a clear nomenclature for apical sensillae of the terminal segment of the maxillary palpus and the laciniogaleae, but did not offer terminology for more basal setae or sensillae of the maxilla. The setae of the thoracic legs were labelled in part by



DC2, dorsal subprimary seta of coxa; fe, femur; FE1–FE2, femoral setae; MC1, proprioceptor seta of anterior coxal sclerite; MTR1–MTR3, proprioceptor setae of trochanter; MTRa, antero-dorsal pore of trochanter; ti, tibia; T11–T16, tibial setae; tr, trochanter; ts, tarsus; TS1–TS4, tarsal setae.

Gerasimov (1952), but his system was not closely or consistently followed by recent treatments (Nielsen and Kristensen, 1989; Miller, 1991).

Chaetotaxal nomenclature adopted here follows the Hinton system (1946) as summarized by Stehr (1987) but agrees with Singh and Goel's (1987) interpretation of subdorsal abdominal setae. Nomenclature of setae and pores on the prothorax follows Hinton (1946), not Hasenfuss (1963), and the names of those on abdominal segment 10 follows Stehr (1987). Terminology for the mandibles follows Gerasimov (1952) and Godfrey (1972); that for the hypopharyngeal complex follows Godfrey (1972). Names for setae and pores of the antenna, maxilla, and labium follow Gerasimov (1952) where possible, conflicting with Grimes and Neunzig (1986b) only with respect to three setae (*sensillae*) of the laciniogalea. Finally nomenclature for the setae and pores of the thoracic legs follows Gerasimov (1952) in part, differing from the systems proposed by Miller (1991) and Nielsen and Kristensen (1989).

Names and symbols for setae newly applied in this paper are in agreement with general principles of a system first introduced by Hinton (1946). His nomenclature based on relative morphological position may be rendered useful, informative, and straightforward by attention to synonymy, homonymy, and priority of usage by earlier authors. Numbering of setae within groups follows general trends and facilitates rapid and accurate recognition of setae: ontogenetic appearance, anterior to posterior, dorsal to ventral, medial to lateral, and sequential continuity around circular or cylindrical structures. Where possible, symbols for setae and pores are chosen as mnemonic abbreviations of the names they represent. Abbreviations for a few head setae have been changed from those of Hinton to avoid homonymy with those on other body parts, but the L and MD setae of the head and body are still homonymous. Finally, symbols for setae and pores are entirely upper case followed by numbers for setae and lower case letters for pores; symbols for sutures, sclerites, and other structures and regions are lower case with the exception of traditional symbols for segments, T1–T3, Ab1–Ab10.

**Head:** Figures 28–29. Only a single substemmatal pore and a single genal proprioceptor seta on each side of head; six labral setae (here symbolized LR1–LR6 following a peripheral sequence, medial to lateral, around each labral lobe) but no obvious labral pores; three stout but otherwise unmodified epipharyngeal setae.

**Antenna:** Figure 32.

**Mandible:** Figure 30. Three distinct apical teeth are subtended by three inner ridges, the first ridge as numbered here originates from the posterior side of a truncate, inner mandibular tooth; a tiny subapical cleft present where outer (posterior) mandibular ridge joins distal margin of mandible.

**Maxilla:** Figure 33. Nomenclature for apical setae follows Gerasimov (1952), MX5–MX7, equalling STIII to STI of Grimes and Neunzig (1986b); pore MPC is the same as Mxj of Gerasimov (1952) and the sensillum digitiformium (SD) of Grimes and Neunzig (1986a).

**Hypopharyngeal complex:** Figure 31. Proximolateral spinules long, well developed; medial surface of hypopharynx smooth; transverse cleft indistinct, not sharply incised.

**Labium:** Figure 31, 33. Nomenclature for divisions of the mentum follows Snodgrass (1935). Spinneret almost as wide as long, membranous, broadly tubular.

**Thorax:** Figure 34. Two SV setae on segment T1, and one SV seta on segments T2–T3. Seta L2 on segment T1 and seta SD1 on segments T1–T3 are very attenuated,

straight sensillae borne in darkly pigmented pits with densely microtrichiated walls (tonosensillae: Rawlins, 1984). These setae are receptors of airborne sound in noctodontid larvae (Tautz and Markl, 1978).

**Abdomen:** Figures 34–35. Four SV setae present on segment Ab10, three SV setae present on segments A2–A6, two SV setae present on segments Ab1, Ab7, and Ab8, and one SV seta present on segment Ab9. Seta L1 posterior to spiracle on segments Ab1–Ab6 and Ab8; below spiracle on segment Ab7; spiracles subequal on segments Ab1–Ab7, enlarged on Ab8; seta SD1 on segment Ab9 normal in size and shape, not a tonosensillum.

**Thoracic legs:** (Figs. 36–37). Coxa divided into anterior and posterior sclerites by an anteroventral coxal suture extended as coxal condyle articulating with trochanter; five primary coxal setae present, one (C1) on anterior coxal sclerite, and four (C2–C5) on posterior coxal sclerite, numbered in continuous sequence around coxa; one small (or proprioceptor) seta on basal edge of anterior coxal sclerite near coxal suture (MC1); one reduced, subprimary seta basal to seta C1 (DC1), and similar reduced seta (DC2) basal to seta C5. Three proprioceptor setae in membranous gap between trochanter and base of femur, numbered sequentially around segment from a relatively anterodorsal position dorsal to coxal suture (MTR1), to an anteroventral position below coxal suture (MTR2), to a posteroventral position (MTR3); a pore (MTRa) situated between seta MTR1 and point opposite coxal suture. Femur without pores; with two setae, anterior (FE1) and posterior (FE2). Tibia with a single posterodorsal pore (Tla) and six setae encircling apex, numbered as Gerasimov (1952) in a continual sequence: anterodorsal (T11), anterolateral (T12), anteroventral (T13), posteroventral (T14), posterolateral (T15), posterodorsal (T16). Tarsus with four setae, numbered as the tibia: anterodorsal (TS1, a small seta), anteroventral (TS2), posteroventral (TS3, just distad of TS2), and posterodorsal (TS4, larger than TS1); setae TS2 and TS3 stout, slightly flattened and bladelike.

**Discussion.** Three features of the chaetotaxy of *Aucula franclemonti* deserve special emphasis: the presence of two SV setae on segment Ab1, two SV setae on segment Ab7, and a normal, non-attenuated seta SD1 on segment Ab9. The number of SV setae on the first abdominal segment has been an important character in the classification of Lepidoptera larvae, noctuid and otherwise. The significance of three SV setae on Ab1 was stressed by Gardner (1946, 1948) and by Crumb (1956) in recognizing several subfamilies of Noctuidae (all Catocalinae *sensu lato*, Herminiinae, Bagisarinae, and Hypeninae) as well as several species of Plusiinae, Acontiinae *sensu lato* (nearctic species of *Lithacodia* and *Eublemma*), and Amphipyrinae (species variously placed by authors in *Perigea*, *Platysenta*, *Condica*, and *Leuconycta*). All agaristine larvae examined in this study had two SV setae on Ab1, the usual condition for the “trifid” subfamilies.

The presence of two SV setae on segment Ab7 appears to be a diagnostic feature of most Agaristinae, and it was utilized in a key to subfamilies for North American species by Crumb (1956). I have examined larvae of species worldwide (listed above), and all have two SV setae on Ab7 except those of *Psychomorpha epimenis*, a North American species placed in the Agaristinae without comment by Crumb (1956). Only a single SV seta was found on Ab7 in noctuid taxa of controversial affinities, including those known to have additional SV setae on thoracic or other abdominal segments: *Litoprosopus futilis* (Grote and Robinson), *Diaphone eumela* (Stoll), *Xanthopastis*

*timais* (Cramer), *Diphthera festiva* (Fabricius). The second SV seta on Ab7 is absent in first instar larvae of Agaristinae, and its presence in subsequent instars appears to be an excellent synapomorphy of most species in the subfamily.

Two SV setae have been observed on Ab7 of the very similar larvae of New World *Bagisara* species (*B. rectifascia* (Grote) and *B. repanda* (Fabricius)) and Old World *Xanthodes transversa* Guenée. The former genus is placed by most authors in Acontiinae, and the latter in Chloephorinae by Poole (1989), but both may best be treated as a distinct taxon, Bagisarinae (or Bagisarini of the Acontiinae), as established by Crumb (1956). The additional subventral seta on Ab7 in both subfamilies is always smaller than the usual subventral seta (SV1), anterior to it, and never on the same pinaculum.

In agaristines the additional seta is always distinctly dorsal to the level of SV1, in a position spatially identical to that of setae SV2 on the first and second abdominal segments, and is therefore labelled SV2. In most agaristines, SV2 on Ab7 is slightly dorsal to SV1, but in *T. chrysochlora* SV2 is positioned so far dorsad that its pinaculum is fused with that of seta L3.

In bagisarines, the additional subventral seta on Ab7 is far ventrad of SV1, and may be almost as close to the ventral midline as seta V1 in a position spatially similar to that of SV3 on the second abdominal segment. This seta in bagisarines should be labelled SV3, and is not considered homologous to SV2 in agaristines.

*Aucula franclemonti* and all other Agaristinae examined lack a tonosensillum on segment Ab9. As on the thorax, the seta that is modified into a tonosensillum is SD1. The presence of this tonosensillum in many "trifid" noctuids (Abrostolini, Amphipyrinae, Cuculliinae, Glottulini, Hadeninae, Heliothinae, Noctuinae, Stiriini), but not in other Noctuoidea, suggests that it may be synapomorphic for a major lineage of Noctuidae. A comprehensive, worldwide survey of this setal modification has not been undertaken, but its absence in Agaristinae does not support their inclusion in an extensive "trifid" lineage bearing the modified seta.

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## TWENTY YEARS OF FLUCTUATING PARAPATRY AND THE QUESTION OF COMPETITIVE EXCLUSION IN THE BUTTERFLIES *PONTIA OCCIDENTALIS* AND *P. PROTODICE* (LEPIDOPTERA: PIERIDAE)

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*Abstract.*—The sibling species *Pontia protodice* and *P. occidentalis* occur on altitudinal gradient across the Sierra Nevada in California, with a mid-elevation belt on the west slope in which neither is a permanent resident. A similar pattern occurs in a variety of unrelated butterfly genera. Studies of the occurrence and breeding of the two *Pontia* across the Sierra for 20 years fail to demonstrate any association (positive or negative) between them in the “no man’s land” on the west slope, thus arguing against competitive exclusion as the mechanism maintaining the separation. Occurrence of *P. protodice* at 1,500 m and 2,100 m is also independent, implying that its presence in the montane Sierra is not simply an epiphenomenon of outflow from a single source in the lowlands. 1991 was an unusual year in which the entire region was colonized, seemingly in a wave emanating from the east. Sporadic competition between the species is not ruled out by these findings, but is unlikely to be important.

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Claims that “Competition from X limited the distribution of Y” used to be common in the ecological literature, but the days when they could be flung about with great abandon are over (Begon et al., 1990). That does not, however, remove the inherent seductiveness of competition-based explanations for community structure. In western North America a repeating pattern exists of altitudinally parapatric sibling species pairs (rarely triplets) of butterflies for which competitive-exclusion explanations appear attractive (Shapiro et al., 1981). In the Sierra Nevada this pattern includes *Everes comyntas* (Godart) and *E. amyntula* (Bdv.) and *L. helleoides* (Bdv.) and *L. nivalis* (Bdv.) (Lycaenidae), *Phyciodes campestris* (Behr) and *P. montana* (Behr) (Nymphalidae), *Anthocharis sara* Lucas and *A. stella* (W. H. Edwards) and *Pontia protodice* (Bdv. & LeC.) and *P. occidentalis* (Reakirt) (Pieridae), *Thorybes pylades* (Scudder), *T. diversus* Bell, and *T. mexicana* (H.-S.) ssp., and *Polites sabuleti* (Bdv.) and *P. tecumseh* (Grinnell) (Hesperiidae), and others. In each case a widespread low-elevation species (the first named) is replaced in the higher Sierra by a closely-related entity of more or less ambiguous (species or subspecies) status, with a band at mid-elevation (1,300–1,700 m) in which neither occurs (or, in the *Thorybes* case, a third species occurs). Shapiro et al. (1981) were the first to point out the “natural experiment” in northern California, where the Sierran endemics *Phyciodes montana* and *Anthocharis stella* do not occur, and *P. campestris* and *A. sara* move upslope and fill more or less of the montane niches occupied by their congeners in the Sierra. This situation suggests either competitive exclusion in the Sierra or its obverse, competitive release, in the northern mountains.

Since 1972 detailed phenological data on all butterfly species have been taken along a transect parallel to Interstate Highway 80, from sea level across the Sierra Nevada

via a series of sampling stations over the crest to mid-elevation on the east slope. Each station is sampled at roughly two-week intervals in good weather whenever there is no significant snow cover; all butterfly species observed are recorded. This program is designed to permit an assessment of the spatial and temporal stability and patterning of the faunas. The data document the fluctuating parapatry across the west slope "no man's land" as well as fluctuating sympatry on the east slope in several species pairs. This paper considers the transect data on *Pontia protodice* and *P. occidentalis* and their relevance to the competitive exclusion hypothesis.

#### THE ORGANISMS

*Pontia protodice* and *P. occidentalis* are sufficiently similar morphologically to be confounded in virtually all museum and many private collections, as well as in many published works. Although Reakirt and W. H. Edwards were clear in their concepts of the species, most subsequent Lepidopterists were not. The nadir of confusion was reached by Abbott et al. (1960), who confounded *all* the North American *Pontia*, but Hovanitz (1962) mapped the distributions of *P. protodice* and *P. occidentalis* reasonably accurately, and Chang (1963) provided diagnostic morphological characters for them. Following several years of field and laboratory studies of their ecology, physiology and variation, Shapiro (1976) reviewed the status of all Nearctic names in the group and concluded that these two were amply distinct at the species level. He also concluded that the entity *nelsoni* (W. H. Edwards) from subarctic Alaska was conspecific with *occidentalis* and that both were probably conspecific with the Palearctic *P. callidice* (Hbn.) complex, which extends from the Alps and Pyrenees eastward to northeast Siberia as a series of disjunct, mostly high montane-alpine populations. According to Shapiro (*loc. cit.*): "(*Pontia*) *occidentalis* occurs upslope and northward of *P. protodice* in western North America. The two species have been found sympatric at various locations from 1000–2500m in the Rocky Mountains and Sierra Nevada, e.g., Donner Pass, California, where *P. occidentalis* is a permanent resident and *P. protodice* a breeding immigrant. . . . In areas of sympatry occasional interspecific matings may occur, but only 2 of 339 specimens collected at Donner Pass in 1973 were phenotypically ambiguous." Shapiro and Geiger (1986), using California populations including sympatric ones along the I-80 transect, demonstrated electrophoretically that they are distinct species and found no evidence for hybridization at Sierra Valley, where they are in massive contact. However, hybridization appears fairly frequent in Colorado (J. Kingsolver, D. Wiernasz, pers. comm.).

Both species occur only in non-forested environments, including tundra, grassland, high desert and steppe; *P. protodice* extends to low (hot) desert. In areas of sympatry, the two species often swarm in dense, mixed flights, breeding on weedy mustards in grain fields and by roadsides. The life cycles of both are very similar, though diagnostic differences exist in the larva and pupa (Shapiro, 1976). Both species are multivoltine (except *P. occidentalis* at the highest elevations) and feed on a variety of Cruciferae, both native and introduced. Both are highly vagile, colonizing species, and *P. occidentalis* has a "hilltopping" epigamic strategy (Shapiro 1975, 1978).

#### THE DATA

Tables 1, 2 and 4 present the occurrence of both species at the Sierran stations along the I-80 transect: Lang Crossing, Nevada Co., ±1,500 m (LC); Donner Pass,

Table 1. Occurrence and breeding of *Poncia protodice* at Lang Crossing (LC), Donner Pass (DP), and Castle Peak (CP), 1972-1991.

Year	LC (1,500 m)	DP (2,100 m)		CP (2,700 m)
1972 <sup>a</sup>	1♀, x.4	1♂, 2♀, ix.7		
1973	—	1♂, vi.27, through ix.28, BRED	—	—
1974	1♀, ix.25	—	—	—
1975	—	2♂, ix.13; 1♀, ix.25	—	—
1976	1♂, viii.13	1♂, viii.20, through xi.20, BRED	—	—
1977	1♀, iv.17	1♂, iv.22	—	—
1978	1♀, vi.15, through x.20, BRED	3♂, vii.1, through x.13, BRED	—	—
1979	1♀, vi.9, through xi.5, BRED	1♂, ix.12; 1♀, x.27	—	—
1980	1♂, viii.19; 1♀, viii.30	—	—	—
1981	1♂, viii.4, through x.6, BRED	2♀, ix.27; 1♂, x.10	—	—
1982	—	1♂, viii.31; 1♀, ix.6; 1♀, ix.12	—	—
1983	1♀, vi.5; 1♀, ix.12	2♀, ix.1	—	—
1984	—	1♂, 1♀, ix.14; 1♀, ix.28	—	—
1985	1♀, vi.24; 1♂, viii.13	3♀, vii.20; 1♂, x.10	—	—
1986	1♂, 1♀, vi.10	4♂, 2♀, vi.19, through ix.4, BRED	—	—
1987	1♂, 1♀, vii.20	1 larva, vii.18	—	1♀, viii.26
1988	2♂, 1♀, vi.16, through x.12, BRED	—	—	1♀, vii.9; 2♂, ix.10
1989	1♀, ix.23	2♂, 1♀, viii.14; 1♂, viii.15	—	—
1990	1♂, ix.5; 1♀, x.12	5♂, 3♀, vii.19, through ix.28, BRED	—	—
1991	2♂, vii.28, through ix.20, BRED	1♂, vi.21, through x.5, BRED	1♂, 1♀, vii.3; 1♀, viii.2	—

<sup>a</sup> Sampling stations were moved a few km in 1973 and remained in their new sites thereafter.

Table 2. Occurrence and breeding of *Pontia occidentalis* at Lang Crossing (LC), 1972–1991. This species has been present and breeding in all years at DP and CP.

Year	LC (1,500 m)
1972	—
1973	—
1974	—
1975	1♀, viii.13
1976	—
1977	1♀, iv.17 <sup>a</sup>
1978	2♂, 1♀, viii.17; 1♂, ix.14; 1♀, x.6; BRED
1979	—
1980	2♀, vii.14; 1♂, viii.4 <sup>b</sup> ; 10♂, 3♀, viii.26; 1♂, ix.10; BRED
1981	—
1982	—
1983	1♀, ix.12
1984	—
1985	—
1986	—
1987	1♂, 1♀, vii.20; 1♂, ix.7; BRED
1988	1♀, vii.22
1989	1♀, vi.22; 1♀, vii.17; 1♀, viii.5; 1♂, viii.16; BRED
1990	—
1991	—

<sup>a</sup> Implies colonization and overwintering undetected in 1976.

<sup>b</sup> Apparent hybrid.

Nevada and Placer Cos., ±2,100 m (DP); Castle Peak, Nevada Co., ±2,700 m (CP); and Sierra Valley, Sierra Co., ±1,500 m (SV). Lang Crossing is a west-slope locality with a mosaic of mixed mesic forest, montane chaparral and Canyon Live Oak xeric woodland on metasedimentary balds, and wet and dry meadows. Donner Pass contains mostly upper montane coniferous forest on a mixture of granite and andesite substrates, but is penetrated by a large wet and dry meadow complex and disturbed roadsides and railway rights-of-way which extend completely through the pass, from one slope to the other; these are lined with Crucifers. Castle Peak (Shapiro, 1978) has subalpine coniferous forest and dry alpine fell-fields on andesite. Sierra Valley is a very large wet and dry meadow complex on Pleistocene lake alluvium, with some alfalfa cultivation along the margins. It is hemmed in by coniferous forest to the west (on the east face of the Sierra) and by a low range of volcanic hills to the east, historically covered with open pine forest but now occupied by sagebrush steppe and juniper woodland; beyond these hills lies the Great Basin high desert.

LC and DP have been sampled for 20 years (the sampling stations were moved several km from their 1972 locations to permanent ones in 1973). CP has been sampled for 20 years, but only 4–6 times/year due to its short flight season. SV was sampled sporadically before 1980 and systematically thereafter, but early-spring data (including the very early flight periods of post-diapause *Pontia*) were obtained only since 1985.

Host plants recorded at the transect stations are presented in Table 5.

Table 3. Dates of first records of *Pontia protodice* at Sierra Valley (SV), where the species is apparently always present in summer. In 1988 and 1990 the first (overwintered) brood, "vernalis," was recorded in April, and the second date corresponds to other years as the beginning of the summer flight.

Year	First date
1985	vi.20
1986	vii.11
1987	vii.1
1988	iv.14; vi.19
1989	vi.3
1990	iv.12; vii.7
1991	vi.13

The data are divided into "occurrence" and "breeding" years. Unavoidably, this classification is somewhat arbitrary; deciding whether or not breeding has occurred is sometimes not easy. Multiple captures on the same day at the same site are not necessarily indicative of local origin (see discussion of dispersal, below). Interpretation of the data involves: consideration of timing and previous frequency, and intervals of sampling; numbers, condition, and sex-ratio of the animals observed; and appropriateness of phenotype relative to season, both locally and in potential source areas (both species are seasonally polyphenic). By these criteria many multiple records have been interpreted as evidence of immigration rather than breeding from a previously undetected colonist. The reality of undetected colonists, however, is underscored by the discovery on 18 July 1986 of a large larva of *P. protodice* at DP in a year when no adults of that species were seen there. For all years in which breeding is claimed in the tables, the numbers and sexes of adults seen at the first observation are noted. Criteria for recognizing breeding include: direct observation of oviposition and/or early stages; ongoing (essentially continuous) presence of adults over several consecutive samples; presence of newly-emerged or teneral individuals; and appearance of two or more consecutive emergences at intervals appropriate for successive generations *in situ*.

Table 4. Status of both species at all four sites, as fractions of years present or breeding (1986 was not treated as a breeding year for *P. protodice* at DP). For criteria used to assess breeding, see text.

	LC	DP	CP	SV
Occurrence				
<i>P. protodice</i>	15/20	16/20	3/20	10/10
<i>P. occidentalis</i>	8/20	20/20	20/20	10/10
Breeding				
<i>P. protodice</i>	5/20	7/20	0/20	10/10
<i>P. occidentalis</i>	4/20	20/20	20/20	10/10

Table 5. Hosts (all Cruciferae) recorded for *Pontia protodice* (P) and *P. occidentalis* (O) at LC, DP and SV, 1972–1991. Additional hosts occur for O at CP.

	LC	DP	SV
<i>Lepidium virginicum</i> var. <i>pubescens</i> (Greene) Thell.	P, O	P, O	P, O
<i>Lepidium perfoliatum</i> L.			P, O
<i>Sisymbrium altissimum</i> L.	P, O		P, O
<i>Descurainia sophia</i> (L.) Webb		P, O	P, O
<i>Descurainia pinnata</i> (Walt.) Brit.			P, O
<i>Cradaria pubescens</i> (Mey.) Roll.		P, O	P, O
<i>Streptanthus tortuosus</i> Kell.	O	O	

## RESULTS

*Pontia occidentalis* is a permanent resident at DP, CP and SV. This is shown by the predictable occurrence of the vernal, post-diapause brood “*calyce* (W. H. Edwards)” (Shapiro, 1976) shortly after snowmelt, though it flies so early it is easily missed. This is not the case at LC, and it very rarely overwinters there.

*Pontia protodice* is not a permanent resident at LC, DP or CP. Its status at SV is uncertain. It has been common or abundant there in summer, with 2–3 generations, every year for nearly 20 years, but early spring data are only available for seven years and in only two of these was the vernal, post-diapause brood “*vernalis* (W.H. Edwards)” (Shapiro, 1976) observed (Table 3). In the Nevada desert and on the floor of the Sacramento Valley (Shapiro, 1979 and unpublished), *P. protodice* overwinters only locally and sporadically. Failure to detect it in early spring in Sierra Valley may not establish its status in a broader, regional context.

Upslope movement by *P. protodice* on a seasonal basis is strongly supported by circumstantial evidence. In 1991, for example, no *protodice* were seen at SV through 1 June. On 13 June, however, they were abundant and uniformly worn and of the second-brood phenotype that was flying at that time around Reno. Females oviposited on roadside Crucifers. Given the climatic and vegetational differences between Reno

Table 6. Comparisons of observed and (in parentheses) expected frequencies of *P. protodice* (P) and *P. occidentalis* (O) alone and in combination at LC, 1972–1991. Neither distribution differs statistically from mutual independence (unadjusted  $\chi^2$  values;  $\chi^2$  adjusted for continuity also NS).

	P +	P -
Occurrence		
O +	7 (6)	1 (2)
O -	- 8 (9)	4 (3)
	$\chi^2 = 1.055$ , NS	
Breeding		
O +	2 (1)	2 (3)
O -	3 (4)	13 (12)
	$\chi^2 = 1.67$ , NS	

Table 7. Comparisons of observed and (in parentheses) expected frequencies of occurrence and breeding of *P. protodice* at LC vs. DP. (These are unadjusted  $\chi^2$ ; adjusted  $\chi^2$  are NS for both comparisons,  $\chi^2_{\text{adjbreeding}} = 1.18$ .)

	LC +	LC -
Occurrence		
DP +	12 (12.75)	5 (4.25)
DP -	3 (2.25)	0 (0.75)
$\chi^2 = 1.54, \text{NS}$		
Breeding		
DP +	3 (1.50)	3 (4.50)
DP -	2 (3.50)	12 (10.50)
$\chi^2 = 2.96, .05 < P < .10$		

and SV, this apparent synchronization is unlikely to be coincidental. On 21 June a male of this phenotype, in poor condition, was taken at DP. On 18 June both sexes were common between Gardnerville, NV and Woodfords, Alpine Co., CA and along the Kingsbury Grade highway to South Lake Tahoe, where they were flying upslope along the roadside. This sort of movement seems to occur every year, albeit usually less conspicuously, and could account for the abundance and reliable occurrence of *P. protodice* at SV each year without overwintering.

What can 20 years of occurrence and breeding data along our transect tell us? Given that neither species persists at LC, that site is particularly important as a potential indicator of competitive exclusion: is the occurrence of the two species either positively or negatively correlated? A negative association could imply either competitive exclusion or reciprocal conditions for colonization (without regard to competition—for example, wet years might favor one species, dry years the other). A positive association would argue against competitive exclusion, suggesting that the same conditions favor colonization by both. There is a single remarkable record of a long-range dispersal by *P. occidentalis*, resulting in its capture in prime *P. protodice* habitat near sea level (Shapiro, 1977)—suggesting that the two species have similar habitat preferences as expressed in active habitat selection.

Table 6 shows that both occurrence and breeding data do not differ significantly from the values expected if the two species were completely independent.

Also of interest is the extent to which occurrence and breeding of the two species are linked among LC, DP and CP. If occurrence at these sites is an epiphenomenon of dispersal from a uniform source (either east or west of the Sierra) we would expect a strong association, while colonization from both sides would produce much weaker association unless population densities in both potential source regions were tightly coupled. Table 7 does not indicate strong association among sites. Mere occurrence is indistinguishable from independence between LC and DP, while the hint of association for breeding is entirely due to 1991 (and disappears if that year is not considered). 1991 was in fact a very unusual year for *P. protodice*. As Table 1 indicates, it did eventually show up at LC and breed there. But it continued spreading westward into the lower foothills, where it merged with an already established population in

the Sacramento Valley; 1991 was the first year since 1977 in which *P. protodice* spread very widely (it reached the Oregon border in Modoc and Siskiyou Counties) and the only year in the history of the transect that it occurred at all ten stations. *P. protodice* is so rare at CP (Table 1) that no analysis is feasible, or necessary, beyond noting that 1988 and 1991 were breeding years at DP, while 1986 was marked by only the single larva mentioned above.

These data thus give no support to competitive exclusion as the cause of either the "no man's land" on the Sierran west slope or the altitudinal stratification of *Pontia* overall. It must be stressed that the sort of comparison done here is not powerful enough to detect competition itself; it can only be suggestive. Nor do these results rule out the possibility of local competition arising as a consequence of the spatial pattern of egg dispersion on hosts (Shapiro, 1975), with no larger-scale impact on distribution.

As Begon et al. (1990) point out, it may not be possible to exclude *prior* competition and character displacement as factors leading to contemporary patterns of replacement or apparent exclusion. Unless that hypothesis is testable, however, it is not very interesting. Altitudinal parapatry is a common pattern in a variety of organisms. In the tropical Andes much more complex patterns can be found in butterflies than occur in the Sierra Nevada (Adams, 1973). Because these patterns could be involved in the process of speciation, it is important to understand how they are maintained; so far there is no persuasive evidence that competition is involved—in *Pontia* or otherwise.

#### ACKNOWLEDGMENTS

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**HYDROPSYCHE FRANCLEONTI, A NEW SPECIES OF  
THE SCALARIS GROUP FROM EASTERN NORTH AMERICA  
(TRICHOPTERA: HYDROPSYCHIDAE)**

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*Abstract.*—The new hydropsychid caddisfly, *Hydropsyche franclemonti*, is described, illustrated and its distribution plotted (Connecticut, New York, North and South Carolina, Virginia and Quebec). It is differentiated from its closest relatives in the *scalaris* group, *H. rossi* and *H. mississippiensis*, and their distributional patterns are discussed.

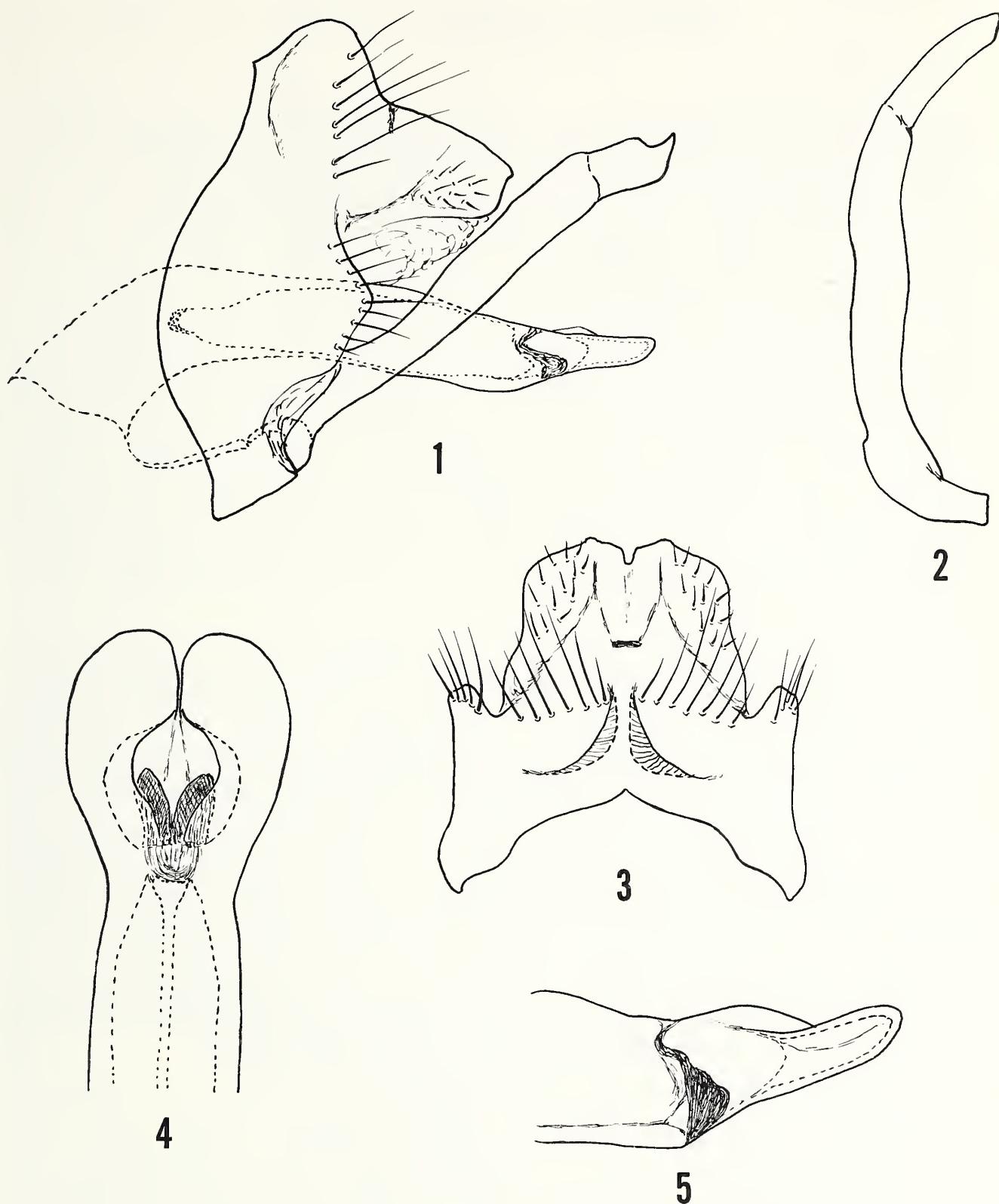
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The genus *Hydropsyche*, as it has been classically recognized, is found on most continents of the world except for South America. However, recent works have established separate genera (or subgenera) for many of the more distinctive groups (Li and Tian, 1989; Neboiss, 1986; Ross and Unzicker, 1977). This has led to a great deal of controversy and confusion in the literature (Schefter, Wiggins and Unzicker, 1986; Schuster, 1984) with the outcome still undecided pending a world-wide, full-scale, revisionary study of all related species groups including their immature stages.

In America north of Mexico the species of *Hydropsyche* were placed into four species groups by Ross (1944), a procedure followed by Nimmo (1987) who recognized three groups, with one group subdivided into six subgroups. Ross christened one of his groups as the *scalaris* group ("species group one" of Nimmo), and placed 13 species from eastern North America therein (another 5 eastern and 5 western species in his 1944 checklist would also be placed in the group). There are no European species clearly belonging to the group, although the species related to *H. pellucidula* are similar but nevertheless different on the basis of the shape of the tenth tergum and apex of the phallus. Surprisingly, I am unable to find any illustrations of species from Japan and China that would appear to be of species close to this group. Thus, at this moment, the *scalaris* group appears to be restricted to North America with one or two species in northern Mexico, a half dozen species in the western United States and Canada, and another several dozen in the eastern United States. The greatest number of species appears to be found in the Mississippi Valley, the Atlantic Coastal Plain and Piedmont Regions. The number of species declines rapidly north of Mason-Dixon Line, with only nine found north of the Canadian border (Nimmo, 1987).

The identification of the species in this group has been difficult, and misidentifications were (and still are) commonplace until Ross (1944) presented detailed illustrations of most of the eastern species. Even in 1979 in our study (Flint, Voshell and Parker, 1979) of the *scalaris* group in Virginia it was necessary to borrow types of most species to verify identifications which then uncovered a major misidentification by Ross in 1944. More recent studies of problematic material have produced yet another species which was either not present or misidentified in older material.

I take great pleasure in dedicating this new species to Dr. J. G. Franclemont who



Figs. 1-5. *Hydropsyche franclemonti*, male genitalia. 1. Lateral. 2. Clasper, posteroventral. 3. Ninth and tenth terga, dorsal. 4. Apex of phallus, ventral. 5. Same, lateral.

encouraged my studies on the Trichoptera at Cornell. His extensive collecting over much of the range of this species in eastern North America—North Carolina, Virginia, New York—while it never turned up this species, did provide many valuable records and range extensions in the Trichoptera.

**Hydropsyche franclemonti**, new species  
Figs. 1–5

*Diagnosis.* This species is a member of the *Hydropsyche scalaris* group (sensu Ross, 1944). It belongs to that subgroup of species whose apical clasper segment is blunt in posteroventral aspect, and whose mesal cavity of the phallus is widely open. In this subgroup are placed *Hydropsyche rossi* Flint, Voshell & Parker and *H. mississippiensis* Flint. The tenth tergum of *H. rossi* in lateral aspect differs in having the dorsal margin nearly straight with the apicodorsal angle slightly prolonged and especially in the apex of the phallus. The inner margin of the lateral flange of the mesal cavity of the phallus in *H. rossi* is, in ventral aspect, very narrow with that portion of the lateral flange beyond the mesal cavity also narrow and of uniform width throughout. The lateral aspect of the tip of the phallus and the apex of the clasper in posteroventral aspect are almost identical in *H. rossi* and *H. franclemonti*. In *H. mississippiensis* the tenth tergum and ventral aspect of the tip of the phallus are more similar to *H. franclemonti* in appearance. However, the apical segment of the clasper of *H. mississippiensis* in posteroventral aspect is bluntly rounded, and the tip of the phallus in lateral aspect has a high mesal dome with the lateral flange close to the midline.

*Description.* Length of forewing, 9.5–10.5 mm. Color brown; forewing mottled, spotted with various shades of brown, as typical of most species of the genus. Eyes of male very large; in frontal aspect each eye equal to the interocular distance. Male genitalia: Ninth segment with anterior margin slightly rounded; with dorsal crest pronounced, strongly compressed, dorsal margin almost semicircular. Tenth tergum in lateral aspect with dorsal margin declivous, apical margin almost vertical with very small apicodorsal bump; in dorsal aspect apex obliquely truncate, with small apicomesal excision. Clasper with basal segment long, slender, slightly sinuous; apical segment in lateral aspect with tip pointed, sharply curved dorsad, in posteroventral aspect with apex obliquely truncate. Phallus tubular, phallobase not constricted before lateral flanges; apex in lateral aspect with mesal dome slightly elevated, lateral flange long, with ventral margin ascendant, tip rounded; in ventral aspect with inner margin of lateral flange broad basally, tapering rapidly apicad, with mesal cavity thus wide open apicad, lateral flange rounded laterally, much widened apicad.

*Type material.* Holotype, male: Virginia, Culpepper Co., Hazel River, off Rt. 707, 3 July 1981, B. C. Kondratieff (NMNH). Paratypes: Same data, except 14 July 1979, 1 ♂ (NMNH). Connecticut, Litchfield Co., Housatonic Meadows State Park, 21–24 May 1983, Rodrigo Andrade, 4 ♂, 2 ♀ (NMNH, YU). New York, Delaware Co., Beaverkill River near Horton, 13 June 1987, P. W. Schefter and R. MacCulloch, 1 ♂, 2 ♀ (ROM). N.C. [North Carolina], Collection Morrison, 1 ♂ (NMNH). South Carolina, Oconee Co., Chattooga River at Burrell's Ford near Route 107, 26–27 May 1981, Ent. 412/612 class, 1 ♂ (CUC). Canada, Prov. Quebec, Station de Biologie de l'Universite de Montreal, St. Hippolyte, 20 June 1973, P. P. Harper, 1 ♂, 4 ♀ (UMDB); Lac Monroe, Parc Provincial du Mont Tremblant, 18 July 1959, J. R. Mougeau & R. Ouellet, 1 ♂, 6 ♀ (UMDB).

*Distribution.* The distributions of the three related species (*H. franclemonti*, *H. mississippiensis* and *H. rossi*), although apparently overlapping to a great part, do

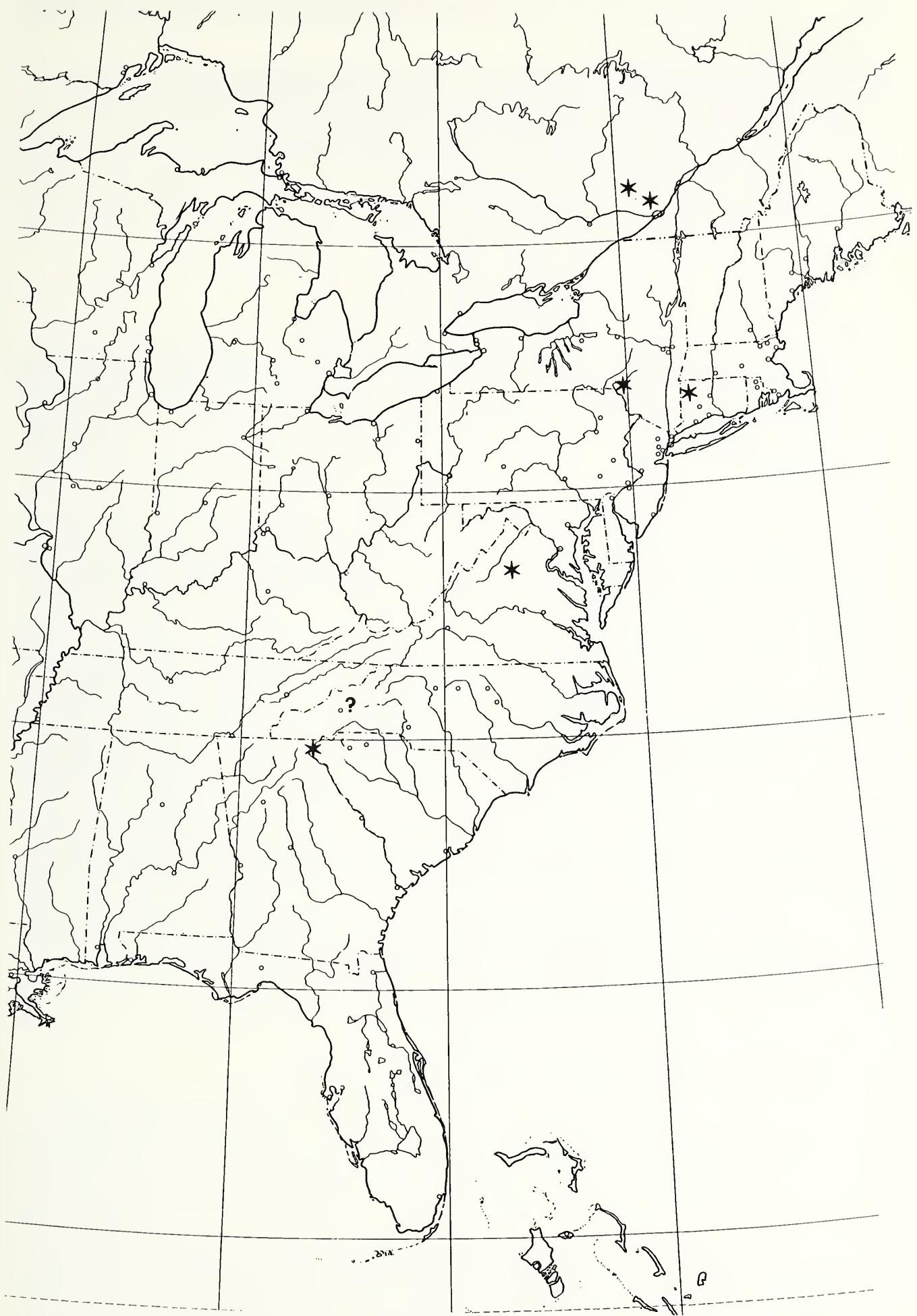


Fig. 6. Known localities for *Hydropsyche franclemonti* (stars); ? placed at Black Mountain, North Carolina, a known site for much of the North Carolina, Morrison, material.

appear to differ in detail. *Hydropsyche rossi* and *H. mississippiensis* are species of the Coastal Plain and lower Piedmont regions. The known range of *H. mississippiensis* extends from Louisiana along the coast north to Virginia, that of *H. rossi* is the same along the eastern coast but extends into Texas along the Gulf and up the Mississippi Valley into Illinois. The range of *H. franclemonti* (Fig. 6), however, appears to follow the eastern margin of the Appalachian Mountains from South Carolina north into Quebec.

#### ACKNOWLEDGMENTS

I am indebted to those who supplied the material of this species: W. G. Downs, Yale University (YU, Connecticut examples), P. W. MacCulloch, Royal Ontario Museum (ROM, New York examples), S. W. Hamilton, Clemson University (CUC, South Carolina example), P. P. Harper, Universite de Montreal (UMDB, Quebec examples) and C. R. Parker and B. C. Kondratieff (Virginia examples).

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## THE TRIBE LICININI (COLEOPTERA: CARABIDAE): A REVIEW OF THE GENUS-GROUPS AND OF THE SPECIES OF SELECTED GENERA

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*Abstract.*—Evidence for monophyly of the Tribe Licinini is found in synapotypic character states of mouthparts (mandibles, primarily reduction of occlusal ridges and grooves) and the head capsule of larvae, with a distinct ventral apotome. Illustrations of mouthparts of adults of representative licinines show four basic types, which distinguish four subtribes: Dicaelina, Dicrochilina (new subtribe), Lestignathina (new subtribe) and Licinina (including the South American genus *Eutogeneius*). Structure of the mandibles and of the fore coxal cavities indicate relationships as follows: Dicaelina + ((Dicrochilina + Lestignathina) + Licinina). A review of the genus *Diplocheila* Brullé reveals for the subgenus *Diplocheila* new synonymy: *Pterostichus* (*Platysma*) *karikali* Jedlička, 1969 = *Diplocheila distinguenda* LaFerté, 1851. A review of the geographical history of subgenus *Isorembus* Jeannel indicates that the *striatopunctata* group was divided in two by opening of the Atlantic Basin, isolating one monophyletic segment in the Nearctic Region, and one in the Palaearctic Region, the latter withdrawing subsequently from Western Europe, and surviving in Western China. Review of recently collected material of the subgenus *Liodicaelus* (gen. *Dicaelus* Bonelli) reveals a new species—*D. franclemonti* (type locality—MEXICO, state of Nuevo Leon, Cerro Potosí, a mountain northwest of Galeana). Re-examination of the type material of *D. l. laevipennis dicaeloides* Ball suggests that this taxon is consubspecific with *D. l. laevipennis* LeConte. The names are synonymized accordingly. Reconstruction of the geographical history of *Liodicaelus* suggests that this lineage is of Late Miocene origin (ca. 12 million years before present), and that differentiation has been the result of vicariance and dispersal, with the oldest barrier between the Sierra Madre Oriental and the Sierra Madre Occidental. Study of the mouthparts of *Badister reflexus* LeConte reveals that, in the West Indies, the mandibles are dimorphic, with either the right or left mandible deeply notched dorsally. This feature of asymmetry was used to diagnose subgenera: left mandible notched, *Baudia* Ragusa; right mandible notched, *Badister* (*sensu stricto*) Clairville. Because it seems clear, now, that the genetic basis for mandibular difference is simple, the groups based on this feature alone should be reassessed.

### DEDICATION

Jack Franclemont was a superb mentor, guiding one along the way by example rather than by precept. It was my good fortune to have been his first graduate student, though it was rumored that on more than one occasion he declared that never again would he have another coleopterist as a student—one of the few promises that he did not keep.

Our association at Cornell was not confined to laboratory and office. I learned under his tutelage that field trips could be civilized and even civilizing experiences, rather than akin to military assault operations. And, on many Sundays, my wife Kay, our two sons and I were invited to his home for dinner—a culinary experience that we valued. But we valued even more Jack's thoughtfulness in extending the invitations.

Kay and I continue to enjoy Jack's company when staying with him in his Snyder Heights home, during our pilgrimages to Ithaca and Cornell. It has occurred to me from time to time that one could spend profitably a sabbatical leave, sitting in his living room, listening to music from his tapes and records, dining at his table, and reading the rich supply of literature that comes to hand so readily.

Nearly 38 years ago, I completed a thesis about classification of licinine carabid beetles. I think that Jack eventually became mildly interested in these fine creatures, though initially he viewed with amused disdain my extolling of their virtues.

On this grand and joyous occasion, as we celebrate Jack's 80 years of life, I am pleased to have the opportunity to dedicate this review to him, with the hope that it will bring back old and hopefully pleasant memories, and that he will find therein some justification for the time and effort that he devoted to making my first review of the licinines a presentable scientific document.

#### INTRODUCTION

Having completed a major treatment of a taxon, systematists tend to seek other taxa, rather than to review again the group that has already been treated extensively—even though a good taxonomic work poses nearly as many questions as it answers. In part, I suppose, after an intensive study of a particular group, one loses a certain amount of interest in it, and in part, at the time of doing the study, one becomes aware of the possibilities at hand in other taxa that are readily accessible to analysis.

After publishing a revision of the North American Licinini (Ball, 1959), I proceeded to investigate other taxa, though two short studies clarified some points that were of special interest to me (El Moursy and Ball, 1959; Ball, 1966b). The idea for the present publication came with the need to offer something suitable for the Franche-mont *Festschrift*. It began with some observations of the West Indian species of the licinine genus *Badister*. With interest in licinines rekindled, I thought about other matters related to *Badister*. Then, because of my interest in Middle American Carabidae, the Mexican species of *Dicaelus* (*Liodicaelus*) came to mind. Certain interesting observations about licinines that I had made during the past 30 years seemed worth including. Previous statements that I had published that proved incorrect required correction. And the mouthparts, especially the mandibles, that seemed of great potential importance in licinine classification and that had not been studied in detail, commended themselves for examination. Collectively, these items constitute a highly eclectic review of licinine Carabidae, their relationships, and geographical distribution.

#### MATERIAL AND METHODS

##### Material

This study is based on detailed examination of about 200 adult licinines, including representatives of the four subtribes recognized and the genera known from North America. Most of the material studied is in the Strickland Museum, Department of Entomology, University of Alberta (UASM). Other collections from which material was borrowed are listed below, along with names of the curators, and a four-letter coden used in the text for identification of the lending institution.

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, U.S.A. 10024 (L. H. Herman);
CASC	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118 (D. H. Kavanaugh);
CMNC	Department of Zoology, Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada (R. S. Anderson);
CNCI	Canadian National Collection of Insects, Biological Resources Division, Centre for Land and Biological Resources Research, K. W. Neatby Building, CEF, Ottawa, Ontario K1A 0C6, Canada (Y. Bousquet);
FSCA	Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Gainesville, Florida, U.S.A. 32601 (R. E. Woodruff);
LSUC	Louisiana State University Insect Collection, Department of Entomology, Louisiana State University, Baton Rouge, Louisiana, U.S.A. 70803 (V. L. Moseley);
MCZC	Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. 02138 (D. G. Furth);
SEMC	Snow Entomological Museum, The University of Kansas, Lawrence, Kansas, U.S.A. 66045-2119 (R. Brooks);
UCBC	Division of Entomology and Parasitology, University of California, Berkeley, California, U.S.A. 94720 (J. Chemsak);
UCDC	The Bohart Museum of Entomology, University of California, Davis, California, U.S.A. 95616 (R. O. Schuster);
USNM	Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. 20560 (T. L. Erwin);
ZMUC	Department of Entomology, Zoological Museum, University of Copenhagen, Universitetsparken, DK-2100, Kobenhavn O. (O. Martin); and
ZSMM	Zoologische Staatssammlung; Münchhausenstrasse 21, D-8000, München 60, Federal Republic of Germany (G. Scherer).

## Methods

Comparative morphology, phylogenetic relationships and classification.—Studies reported are at three hierarchical levels: subtribal, involving groups of genera; subgeneric, and intrasubgeneric; and intraspecific. At the subtribal level, because my principal goals were to assay and describe structural features used previously in classification and to achieve thereby an improved understanding of licinine relationships, I used an exemplar method, i.e., one or a few taxa that were readily available to me, to analyze the characters of a grouping recognized previously. To this study, I added as well published studies of other character systems, including chromosome number, defensive secretions, and characteristics of larvae.

Being interested in phylogenetic relationships as a basis for classification, I attempted to establish transformation series, and to position the licinine taxa accordingly. To polarize the transformation series, I used as outgroup the pterostichine genus *Loxandrus* LeConte, because it seemed to be in most respects less derived

than the licinines, and yet to exhibit some features of the licinine ground plan, such as form of the male fore tarsomeres and having a pair of pits in the ventral surface of the mentum.

For the subgenus *Isorembus* Jeannel, I reviewed a flawed previous effort to establish the phylogenetic relationships of the species groups by using the outgroup method, with the other two subgenera of the genus *Diplocheila* Brullé as outgroups.

For the subgenus *Liodicaelus* Casey, I had the opportunity to undertake a more detailed study, having at hand representatives of all known taxa. However, the data available were not sufficient to permit a very convincing evolutionary treatment, and so I confined my activities to improving means of identifying the taxa and to documenting more fully their geographical ranges. Using essentially the commonality principle in the absence of a clearly specified outgroup, I recognized one species as the probable primitive adelphotaxon of the other four, and postulated that the latter group comprised a monophyletic assemblage.

For the genus *Badister*, I postulated infraspecific dimorphism in mandibular asymmetry of *B. reflexus* LeConte, a character that was regarded by most previous authors as of generic or subgeneric value. To make such a postulate required a further postulate about conspecificity. Recognition of the two mandibular morphs as members of the same species was based on their overall detailed similarity in features (principally male genitalia) whose variation signals specific differences throughout the genus *Badister*.

**Biogeographical analysis.**—For the subgenus *Isorembus* Jeannel and *Liodicaelus* Casey, I commented about their distribution patterns in an evolutionary context. I compared the distribution patterns of these taxa to similar patterns of other taxa that had been analyzed more rigorously, and reasoned by analogy that such similarities reflected similar histories of dispersal and vicariance.

**Measurements.**—These were used to indicate size and proportions for specimens of *Liodicaelus*. The following measurements were made, using an ocular micrometer in a Wild S5 Stereobinocular Microscope, at a magnification of 25 $\times$ :

- length of head—linear distance from base of the left mandible to the posterior margin of the left eye;
- width of head—maximum linear transverse distance across eyes, from outer margin to outer margin;
- length of pronotum—linear distance from anterior (apical) to posterior (basal) margin, measured along the mid-line;
- width of pronotum at apex—linear transverse distance between antero-lateral angles, measured at right angle to the long axis;
- maximum width of pronotum—maximum linear transverse distance across pronotum, measured at right angle to long axis;
- length of elytra—linear distance from basal ridge to elytral apex;
- width of elytra—maximum transverse distance across elytra, measured at right angle to long axis.

These measurements were added or combined in ratios, and designated as follows:

SBL—Standardized Body Length—sum of length of head, pronotum, and elytra;  
EW—width of elytra, and also maximum body width;

PW/HW—width of pronotum/width of head;

PL/PWA—pronotum: length/width at apex;

EL/EW—elytra: length/width

For SBL, PW/HW, PL/PWA and EL/EW, means were calculated and results presented in Tables 3–6. Also, a scattergram was prepared (Fig. 15), based on PL/PWA and EL/EW for discrimination among the species of *Liodicaelus*.

**Dissections.**—These were made using standard techniques. Genitalia were preserved in glycerine, in microvials, pinned beneath the specimens from which these sclerites had been removed. Larger parts, or those that had been gold-coated for study with the Scanning Electron Microscope, were glued to cards, and pinned beneath the specimens from which they had been removed.

**Illustrations.**—A Cambridge S-250 Scanning Electron Microscope was used to examine and photograph gold-coated sclerites. Line drawings were prepared by using a *camera lucida* attached to a Wild S5 Stereobinocular Microscope.

### Terms for structural features

Most of the words used to designate details of structures are found in entomology textbooks or are used by coleopterists, generally. Other words, required to designate particular structures or parts thereof, are not in general use. I provide information about such words here.

**Body parts.**—The term “segment” is restricted to those body parts that reflect embryonic somites. Thus, somite-like portions of the abdomen are referred to as segments. Abdominal segments are designated by a Roman numeral that corresponds to the respective somites. The first complete sternum is III, and the last one that is completely sclerotized and normally exposed is VII.

Portions of limbs are designated by the suffix “-mere,” the prefix depending upon the limb in question—antennal, palpal, tarsal, etc.

**Labium.**—The word “ligula” is used for glossae + paraglossae. In turn, the fused, sclerotized glossae characteristic of carabids are termed the glossal sclerite.

**Elytra.**—Longitudinal grooves on the dorsal surface, or remnants thereof (“striae” of most authors) are designated as interneurs (Erwin, 1974:3–5).

**Ovipositor.**—The terminal parts are referred to as stylomeres. The thick marginal setae on stylomere 2 are ensiform setae.

### Terms for phylogenetic aspects

These are standard, except for “adelphotaxon.” This word was introduced by Ax (1987:36) as a substitute for sister taxon. The advantage of using adelphotaxon is that, being of classical origin, it will be the same in all European languages and thus does not require translation.

### RELATIONSHIPS OF THE LICININI

Jeannel (1941) included in the Callistomorphi the families Callistidae (including the oodines), Licinidae, and Panagaeidae. Kryzhanovskij (1983:88–89), using a more traditional system of ranking, included the tribes Licinini, Callistini, and Oodini in the supertribe Callistitae, placing the Panagaeini in the supertribe Panagaeitae, along

with the Peleciini. Erwin (1985:468) separated also the panagaeines from the Callistitae, including in the Panagaeitae as well the Afrotropical Bascanini and the Peleciini (*sensu latiore*). Considering the shared derived features of callistites (*sensu Kryzhanovskij* and Erwin) and at least panagaeines, exhibited by adults (including paramedian mental pits, and defensive secretions [see below]) and by larvae, it seems best to include the two complexes in a single supertribe. Straneo and Ball (1989:85) placed the peleciines as *incertae sedis*, near the base of the subfamily Harpalinae (*sensu Erwin*, 1985:468).

Within the callistite assemblage, the tribe Licinini probably occupies a basal position—at least such is suggested by the distinctive pattern of volatile organic compounds comprising the defensive secretions of the pygidial glands. A basal position for the Licinini is indicated also by features of the fore coxal cavities—probably plesiotypically uniperforate, whereas oodines, callistines and panagaeines exhibit the probably apotypic feature of biperforate coxal cavities. I postulate the following system of relationships: Licinini + (Oodini + (Callistini + Panagaeini)). See below for details.

#### GENERIC CLASSIFICATION

Important recent references to Licinini are: Darlington (1968:14–19), treating the genera and species of New Guinea; Lindroth (1968:939–944 and 1969:945–967 and 1121), treating the Canadian and Alaskan taxa; Kryzhanovskij (1983:274–276), treating the fauna of the USSR; Freude (1976:254–260), treating the fauna of Middle Europe; and Moore et al. (1987:263–269), cataloguing the Australian taxa.

Freude (1976), evidently following Jeannel (1942), placed *Licinus* and *Badister* in the subfamilies Licinitae and Badisteritae, respectively, thus separating these two genera as widely as either is separated from other carabid subfamilies, such as Pterostichitae and Harpalitae. Such ranking does not coincide with the affinities of these genera, as explained by Ball (1959), and amplified below.

Ball (1959:7) arranged the licinine genera in four groups which he regarded as the equivalent of subtribes. Two were named: *Dicaelina* (Group 1) and *Licinina* (Group 2), leaving Groups 3 and 4 unnamed. They are named here: *Lestignathina* (name based on that of the first described genus included in this group—*Lestignathus* Erichson [1842:132]), new subtribe (Group 3); and *Dicrochilina*, new subtribe (Group 4).

Two genera, the northeastern Australian *Mecynognathus* MacLeay and Chilean *Eutogeneius* Solier (1849:253), were excluded from the classification because Ball had not seen specimens. Jeannel (1942:991) placed the enigmatic *Mecynognathus* in the Licinini because of the strikingly modified mouthparts of the adults. Darlington (1961:18) included *Mecynognathus* in the Tribe Pterostichini, as did Moore (1965: 22), based on overall similarity and chorological affinity to the clearly pterostichine genus *Paranurus* Tschitschérine.

Although I have not studied material of *Eutogeneius fuscus* Solier (1849:255) in great detail, I have seen the holotype in the Oberthür-Chaudoir Collection (Mus. Nat. Hist. Nat., Paris), and two additional specimens in the Canadian National Collection of Insects, Ottawa. A male exhibits adhesive vestiture of articulo-setae on the front tarsus (Stork, 1980:287), and the mandibles are short and broad, with broad apices. On the basis of these observations, *Eutogeneius* is assigned to the subtribe Licinina.

Ball (1959:6–8) used features of the adult mandibles as the primary basis for classifying the licinine genera, but he provided only a superficial account of these structures. A more detailed description of the licinine mandibles is presented below, based on Acorn and Ball (1991). Study of the mouthparts was extended to include the labrum, maxillae, and labium. The adhesive vestiture of the anterior tarsi of males was examined in some detail. Also, a few specimens were examined for the condition of the fore coxal cavities. As noted in the Methods section above, the pterostichine genus *Loxandrus* was used as an out-group.

Based on published information, additional characters for classification were sought in the defensive secretions of adults, in structural features of the larvae, and in chromosome number.

## Mandibles

As explained by Acorn and Ball (1991) carabid mandibles are trigonal in form, each tapered from a broad base to a narrow, more or less pointed apex (Fig. 1A–B). Laterally broad and with a triangular depression in the outer face (the scrobe), the mandible is sloped toward the occlusal surface (Fig. 1C–D), or the edge that opposes the other mandible, and is involved in biting or gripping the food items. In dorsal aspect, two imprecisely defined areas are recognized: a terebra, extending from the apical incisor tooth (Fig. 1A, i) to a transverse plane, extended through the terebral tooth (tt). Posterad the terebra is the broader basal area. A series of ridges and teeth are on the occlusal margin, as follows, anteriorly to posteriorly, and dorsally to ventrally (Fig. 1A–E): incisor tooth; terebral ridge (tr), or if two, superior terebral (str) and inferior terebral (itr); terebral tooth; retinaculum (r), in most groups with teeth (anterior, art, and posterior, prt), and a ridge (rr). The end of the retinaculum is marked in most taxa by a deep groove, the anterior occlusal groove (aog) posterior to which is the molar area, divided or not by a posterior occlusal groove into a more anterior premolar ridge and/or tooth, and a posterior molar ridge and tooth. These distinctions are not required here, and the molar area is designated simply m. Ventrally, a groove extends diagonally or more or less parallel to the occlusal margin—the ventral groove (Figs. 1E–F, vg). Arising from the ventral groove is a brush of microtrichia (vmt).

Mandibles of *Loxandrus* LeConte (Fig. 1A–F).—The terebra occupies about  $\frac{2}{3}$  of the mandible, as is true of most carabid mandibles (Acorn and Ball, 1991). On the left mandible (Fig. 1A, C, E), the superior (str) and inferior (itr) terebral ridges meet at the terebral tooth (tt). The tooth and ridges comprise the occlusal portion of the terebra. Posterad the terebral tooth, the occlusal surface is occupied by the retinaculum, or retinacular ridge (rr) which extends ventrad the terebral ridge. The anterior occlusal groove (aog) at the posterior margin of the retinaculum, is marked distinctly. Posterad the groove is the molar area (m), which in *Loxandrus* is ridged (Fig. 1C), and extends anteriorly as a ridge (Fig. 1F) beneath the retinaculum. The ventral groove (Fig. 1E, vg) is moderately long and its brush is comprised of rather short microtrichia (vmt). The right mandible (Fig. 1B, D, F) is similar to the left except that the retinacular ridge (rr) is more prominent and terminates anteriorly in a pronounced anterior retinacular tooth (art), referred to by Bell (1960:100) as the canine tooth.

Mandibles of representative species of *Chlaenius* are described and illustrated by Bell (1960:163, figs. 122–131). Spence (1982:571, fig. 5A) illustrated mandibles of an oodine. Both groups are characterized by long terebrae, a complete set of teeth and ridges, and occlusal grooves.

By contrast and in general, mandibles of licinine adults exhibit more extensive ventral grooves (Fig. 1K–L, 2E–F, K–L, and 3E–F, K–L), and less complex occlusal margins that lack an occlusal groove separating the molar area from the retinaculum (Figs. 1G–L, 2A–L, 3A–L). The occlusal margin posterad the terebral tooth is named here basal ridge (br), because it is unclear (except in *D. daldorfi*, Fig. 1G–L) how much of this margin is retinacular and how much is molar.

Mandibles of subtribe Dicaelina.—These are illustrated by specimens of *D. daldorfi* Crotch (Fig. 1G–L) and *D. polita* Dejean. See also the mandibles of *Dicaelus* (*Liodicaelus*) (Figs. 13A–L, 14A–F).

The terebral ridge is nearly straight, with the incisor quite broad (Figs. 1G–H, 2A–B). In occlusal aspect (Figs. 1I–J, 2C–D), the terebral surfaces are quite broad and sloped diagonally ventro-laterally. In contrast to *Loxandrus*, dicaeline mandibles are more slender basally. The ventral groove of *Diplocheila* mandibles bears brushes of very long microtrichia (Figs. 1K–L, 2E–F), but the microtrichia are shorter in *Dicaelus* (Figs. 13E–F, K–L, and 14E–F). The dicaeline terebra is about half the length of the mandible.

The terebrae of *D. daldorfi* (Fig. 1G–H) are about as broad as those of *D. polita* (Fig. 2A–B), and the occlusal surface on the right mandible is smooth (Fig. 1J) rather than diagonally ridged, as in *D. polita* (Fig. 2D). The left mandible of *D. daldorfi* exhibits a small supraterebral tooth (Fig. 1G, stt), a unique feature of this species. (Unfortunately, the dorsal surface of the specimen illustrated is worn somewhat, and irregular.) The retinaculum is small (Fig. 1G, I). The right mandible of *D. daldorfi* (Fig. 1H, J) lacks a clearly marked retinaculum.

The left terebral tooth of *D. polita* (Fig. 2A, E) is more prominent, and the left mandible has a small retinacular tooth (Fig. 2A, art) and a rather indistinct retinacular ridge (Fig. 2E).

The left terebral tooth of *D. polita* (Fig. 2A, E) is more prominent; the retinacular tooth is small (Fig. 2A, prt), and the retinacular ridge is rather indistinct. The right mandible (Fig. 2B, D) is without a clearly marked retinaculum.

Mandibles of subtribe Dicrochilina (Fig. 2G–L).—Terebrae are short, not more than one-third the length of the mandibles (Fig. 2G–H), and the basal part is relatively slender (Fig. 2I–J). The terebral teeth (tt) are small, the right one isolated from the superior terebral ridge (str) by a notch. The left mandible exhibits two terebral ridges (Fig. 2G, str and itr). The retinacula are absent. The ventral grooves bear long and densely packed microtrichia (Fig. 2K–L).

Mandibles of subtribe Lestignathina (Fig. 3A–E).—Markedly flattened dorso-ventrally, especially the terebrae (Fig. 3C–D), dorsally these mandibles exhibit broad terebrae, very slender and sharp incisors, and very prominent and sharp terebral teeth (Fig. 3A–B, i and tt). The terebral area is less than half the length of the mandible. Ventral retinacular or molar ridges are not indicated. The microtrichia of the ventral grooves are short (Fig. 3E–F, vmt).

Mandibles of subtribe Licinina (Fig. 3G–L).—These sclerites are very broad, especially basally (Fig. 3G–H, K–L), and thick (Fig. 3I–J). The terebrae are narrow in

the horizontal plane, comparatively short, with occlusal margins nearly straight, and terebral teeth thick and prominent, and incisors blunt (Fig. 3I–J). The basal areas of both mandibles are markedly thickened, especially that of the right mandible, which has also a dorsal boss (Fig. 3I–J, b). The thickened terebral and basal areas of the right mandible are separated from one another by a low area, referred to as a notch (Fig. 3J, n). The left mandible does not exhibit such a notch. Such asymmetry between mandibles is a common feature of the Licinina, some taxa with the right mandible notched, others with the left, and still others with either mandible notched (see below, under *Badister reflexus* LeConte). The ventral grooves have short microtrichia (Fig. 3K–L, vmt).

The mandibles of the Licinina are without retinacular and molar ridges.

Mandibles of *Badister* are illustrated in Figures 19A–H and 20A–F. The terebral ridges of both mandibles are short, and are deflected ventrally, causing the mandibular apices to appear very broad in the anterior aspect (Fig. 20A–B).

#### Labrum (Figs. 4A–I, and 5A–D)

Licinines exhibit variously modified labra, most with a more or less pronounced medial notch. For comparison, illustrations of a more generalized labrum are provided (*Loxandrus pactinillus* Allen, Fig. 4A–B).

Labrum of *Loxandrus* (Fig. 4A–B).—This sclerite is about rectangular, with the anterior margin slightly concave (Fig. 4A), or straight. Dorsally, six long setae form a transverse row near the anterior margin. Ventrally, the labrum bears an epipharynx comprised in carabids of trichoid sensilla (Fig. 4B, ets) flanked each side by a group of microtrichia (Fig. 4F–G, emt). Liebherr (1991a:10–11, and Figs. 2, 8, 14, 20) showed a similar pattern for platynines, and that number of sensilla is correlated positively with body size.

Labrum of subtribe Dicaelina (Fig. 4C–G).—The anterior margin is more or less deeply notched, and in outline the labrum varies from transverse (Fig. 4E) to about quadrate (Fig. 4C). Dorsal setae vary in number from four (Fig. 4C, E) to six. Ventrally, the trichoid sensilla of the epipharynx are long and submarginal, the central part of the labrum being absent. The patches of microtrichia are more (Fig. 4F) or less (Fig. 4D) extensive.

The labra of subgenus *Isorembus* and of genus *Dicaelus* are much less modified, with the anterior margin less deeply and broadly notched, and trichoid sensilla of the epipharynx shorter.

Labrum of subtribe Dicrochilina (Fig. 5A–B).—In outline, the labrum is longer than wide, with anterior margin broadly concave. Dorsally are six marginal setae. Ventrally, the epipharyngeal trichoid sensilla are of average length and number. The microtrichia are numerous, and form a central “Y” figure, with the stem prominent (Fig. 5B, etr).

Labrum of subtribe Lestignathina (Fig. 4H–I).—For the Licinini, the labrum is markedly transverse and short. The central portion is present, and in fact is projected as a small tooth. The dorsal marginal setae number four. Ventrally (Fig. 4I), the trichoid sensilla are few, and the microtrichia are grouped in two small basal patches, one each side of the mid-line.

Although typical of *Siagonyx*, a labrum of this type is atypical for the Lestignathina

as a whole, with adults of the other genera exhibiting a normal licinine labrum, quadrate in outline, with the central area absent.

Labrum of subtribe Licina (Fig. 5C–D).—The form varies appreciably from asymmetric with an irregular anterior margin to symmetric, with a deep central notch (Fig. 20A–B). Dorsally, six setae comprise the marginal row (Fig. 5C). Ventrally, the epipharyngeal trichoid sensilla are few, and microtrichial patches are absent (Fig. 5D).

### Maxillae (Fig. 6A–H)

In form and sclerites present, licinine maxillae are about average for adult carabids. Palpomeres vary in proportions. Vestiture of the lacinia and development of the lacinial tooth seem to offer the most useful features for classification.

Maxillae of subtribe Dicaelina (Fig. 6A–B).—The lacinial tooth (lt) is curved slightly. In dorsal aspect, the occlusal margin of the lacinia has a dense array of slender setae which extends on to the dorsal surface near the apex (Fig. 6A). Ventrally, the occlusal margin has several rows of stout setae which extend on to the ventral surface basally (Fig. 6B). Palpomere 3 (Fig. 6A, mp-3) is subequal in length to palpomere 2 and is distinctly longer than palpomere 4.

Maxillae of subtribe Dicrochilina (Fig. 6C–D).—These are similar to the maxillae of the Dicaelina (see above), except that the lacinial tooth is curved more sharply in relation to the long axis of the lacinia.

Maxillae of subtribe Lestignathina (Fig. 6E–F).—The lacinia exhibits a sinuate lateral margin, is widened apically, and the apical tooth is sharply bent, in fact slightly recurved at apex (Fig. 6E, lt). In dorsal aspect, the slender setae are relatively few and quite short. Ventrally, the stout setae are rather few also (Fig. 6F). (Sparse setation of the lacinia is exhibited also by oodines of the genera *Anatrichis* LeConte and *Oodinus* Motschulsky ([Spence, 1982:572, fig. 7A, B]). Palpomere 3 (Fig. 6E, mp-3) is much shorter than either 2 or 4.

Maxillae of subtribe Licinina (Fig. 6G–H).—The lacinial tooth (Fig. 6G, lt) is very prominent and is bent at a right angle to the long axis of the lacinia. Slender setae are in several not particularly dense rows, and some of them are curved apically. A few setae extend on to the dorsal surface preapically. Ventrally, the stout setae are prominent and in several rows along the occlusal margin. The basal area has few setae (Fig. 6H).

### Labium (Figs. 7A–E and 8A–D)

The licinine labium is characterized by absence of a mental tooth, and by a bisetose glossal sclerite. Other features vary from subtribe to subtribe, as noted below. The bisetose submentum is taxonomically featureless.

Labium of subtribe Dicaelina (Fig. 7A–C).—Separated from the submentum by a complete suture, the mentum is transverse, with broad lateral lobes (11), and epilobes (el) with apices terminated at the apices of the lateral lobes. Ventrally, the mentum has a moderately deep median sinus, and bears a pair of paramedial setae, and near the base a pair of pits (Fig. 7A, mp) with small pores in the surface (Fig. 7C). Allen and Ball (1980:507, fig. 25B) illustrated similar structures for taxa of *Loxandrus*. Mental pits are common in *Chlaenius* (Bell, 1960:100, and 163, figs. 132–135), in

Panagaeini and in the Oodini (Spence, 1982:572, fig. 8A). Bell (1960:100) stated that licinines were without these pits. Their function is unknown, but it seems more likely that they are sense organs rather than "... simply the outward manifestations of inwardly-directed apodemes" (Allen and Ball, 1980:488). The paraglossae (pg) of the prementum are narrow lobes extended beyond the apex of the glossal sclerite (gl). Dorsally, the paraglossae are covered with an extensive vestiture of microtrichia (Fig. 7B), as is true also for the oodine genus *Anatrichis* (Spence, 1982:572, fig. 9A). Palpomere 2 is bisetose.

Labium of subtribe Dicrochilina (Fig. 7D-E).—In general, this complex of sclerites is much like that of the Dicaelina, differing as follows. Lateral lobes (Fig. 7D, ll) are longer, and the apices of the epilobes (el) extend clearly beyond the apices of the lateral lobes. Palpomere 2 is quadrisetose.

Labium of subtribe Lestignathina (Fig. 8A-B).—The mentum is asetose and lacks pits (Fig. 8A). The medial sinus is shallow, so that the medial part is quite broad. The apices of the epilobes (el) are coextensive with the apices of the lateral lobes (ll). The paraglossae (pg) are small, and are not extended beyond the apex of the glossal sclerite (gl), which is convex and is projected anteriorly. Dorsally, the surface of the ligula (paraglossae + glossae) is covered with isodiametric microsculpture, the sculpticells with surfaces convex (Fig. 8B). Each paraglossa has a row of small microtrichia. Palpomere 2 is bisetose.

Mentum and submentum are fused, i.e., the mental suture is absent or incomplete. Horn (1881:143) noted that the mental suture is absent from the specimen of *Lestignathus* that he examined. Sloane (1898:488) pointed out that this suture is absent also from the labia of *Lacordairia*, *Siagonyx*, *Hormacrus*, *Platylytron*, and *Microferonia*. Further, he countered Horn's argument that *Lestignathus* is a platynine rather than a licinine.

Labium of subtribe Licinina (Fig. 8C-D).—The mentum is bisetose (punctures evident near posterior margin of the deep medial sinus, but setae broken), and the ventral surface is without pits (Fig. 8C). Lateral lobes (ll) are average, with apices of epilobes (el) coextensive with apices of lateral lobes. The anterior margin of the glossal sclerite (gl) is slightly convex and slightly projected. For *Licinus*, the paraglossae (pg) are short and broad and not extended beyond the apex of the glossal sclerite. Dorsally, each paraglossa has a covering of long setae apically (Fig. 8D, pts) and a vestiture of microtrichia basally. In contrast, for *Badister*, the paraglossae are substantially longer than the glossal sclerite, and the dorsal surfaces of the paraglossae have a covering of apically broad, flat microtrichia, and marginally, hair-like microtrichia. For both of these genera, palpomere 2 is bisetose.

#### Fore coxal cavities

According to Jeannel (1941:78-82), one of the features diagnostic of the callistomorph assemblage is biperforate fore coxal cavities. This is correct for the Callistini, Oodini, and Panagaeini. However, condition of the fore coxal cavities varies within the Licinini: Dicaelina and Licinina have uniperforate cavities (i.e., a sclerotized bridge dividing each cavity is lacking), but Dicrochilina and Lestignathina have biperforate cavities.

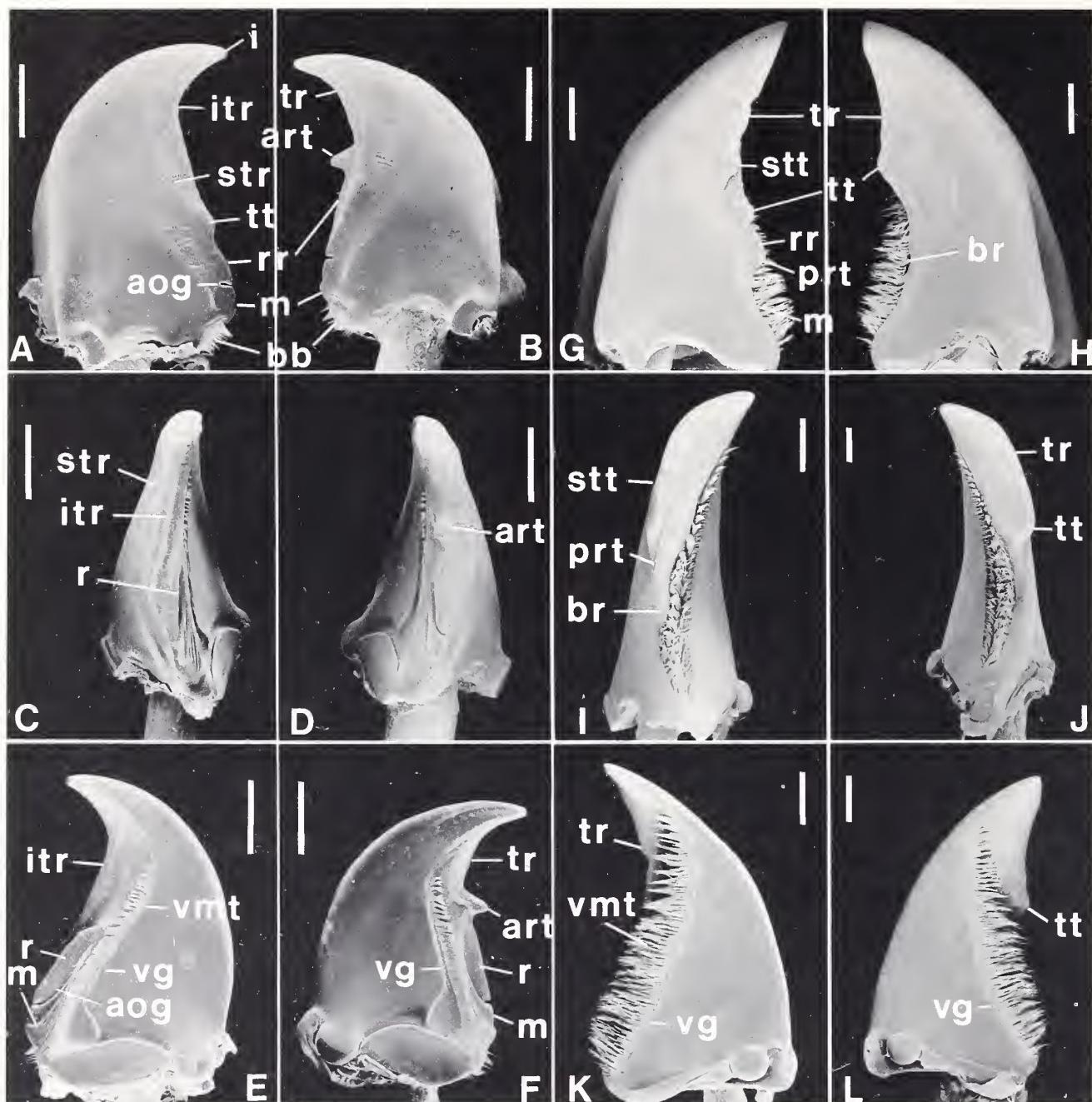


Fig. 1A-L. SEM photographs of mandibles of *Loxandrus pactinillus* Allen and *Diplocheila daldorfi* Crotch. A-F, *L. pactinillus*: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D, and F, right mandible—dorsal, occlusal and ventral aspects, respectively. G-L, *D. daldorfi* Crotch: G, I and K, left mandible—dorsal, occlusal and ventral aspects, respectively; H, J and L, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: aog, anterior occlusal groove; art, anterior retinacular tooth; bb, basal brush; br, basal ridge; i, incisor; itr, inferior terebral ridge; m, molar tooth; prt, posterior retinacular tooth; r, retinaculum; rr, retinacular ridge; str, supraterbral ridge; stt, superior terebral tooth; tt, terebral tooth; vg, ventral groove; vmt, ventral microtrichia. Scale bars: A-F = 200  $\mu\text{m}$ ; G-I = 400  $\mu\text{m}$ .

#### Male fore tarsi and adhesive vestiture (Fig. 9A-I)

A diagnostic feature of the supertribe to which the Licinini belong (Callistomorphi Jeannel, 1941; Kryzhanovskij, 1983; or Patellimanes of 19th Century authors) is size of male fore tarsomeres and their adhesive vestiture. The group is characterized by

Table 1. Defensive compounds secreted by the pygidial glands of adult Licinini, and released by spraying (data from Moore, 1979:195, table 1).

Subtribe	Compounds		
	Formic acid	Hydrocarbons	Aliphatic ketones
Dicaelina <sup>1</sup>	X		
Dicrochilina	X	X	X
Lestignathina <sup>2</sup>	X	X	
Licinina <sup>3</sup>	X	X	

<sup>1</sup> *Dicaelus*, only.

<sup>2</sup> *Siagonyx*, only.

<sup>3</sup> *Licinus* and *Badister*, only.

having at least some of the tarsomeres widened asymmetrically, and with a dense vestiture of adhesive setae, designated articulo-setae by Stork (1980:287). Within the Licinini, size of male fore tarsomeres and extent of vestiture vary appreciably.

Male fore tarsomeres of subtribe Dicaelina (Fig. 9A–C).—Tarsomeres 1–3 slightly expanded on medial side, with typical callistomorph adhesive vestiture ventrally (Fig. 9B–C).

Male fore tarsomeres of subtribe Dicrochilina (Fig. 9D–F).—Tarsomeres 1–3 expanded diagonally medially (Fig. 9D), rather like loxandrine tarsomeres (Allen and Ball, 1980:511, fig. 43A–B). Ventral adhesive vestiture of articulo-setae (Fig. 9E–F), arranged in four diagonal parallel rows on tarsomeres 1 and 2, only two rows on tarsomere 3.

Male fore tarsomeres of subtribe Lestignathina.—In form and vestiture, these are like the tarsomeres of the Dicaelina.

Male fore tarsomeres of subtribe Licinina (Fig. 9G–I).—Tarsomeres 1 and 2 (Fig. 9G) expanded markedly, ventral adhesive vestiture of articulo-setae (Fig. 9H–I) on tarsomeres 1 and 2 (or on 1–3), densely packed.

### Defensive secretions of the Licinini

Moore (1979) compared the defensive secretions of the pygidial glands of a broad taxonomic representation of carabid genera. He reported that callistomorphs produce a wide range of volatile organic compounds: hydrocarbons, aliphatic ketones, saturated esters, formic acid, phenols, aromatic aldehydes, and quinones. From an evolutionary perspective, production of a mixture of hydrocarbons and formic acid probably is plesiotypic for callistomorphs, this feature being widespread in the subfamily Harpalinae, which includes the Callistitiae. Within the latter group, however, only the licinines exhibit this feature: oodines secrete unsaturated acids, only; callistines, hydrocarbons, phenols, and quinone; and panagaeines, hydrocarbons, aliphatic ketones and phenols. Presumably, absence from the defensive repertoire of hydrocarbons and/or formic acid is the result of loss, and the production of other volatile organic compounds is a gain, both being apotypic. Thus, licinines are relatively primitive compared to the other tribes with respect to production of defensive secretions.

The pattern within the Licinini is shown in Table 1. Members of all subtribes

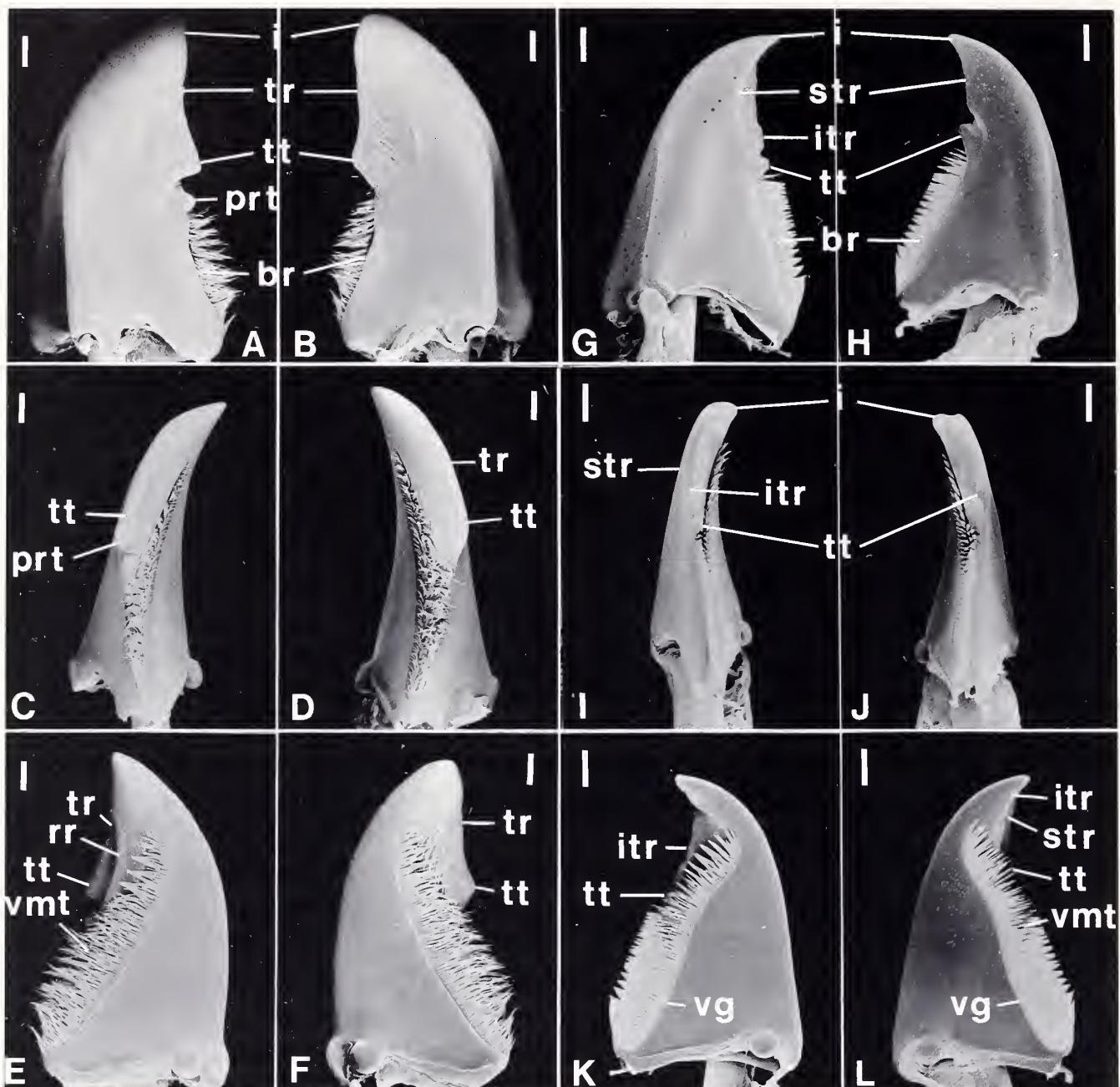


Fig. 2A–L. SEM photographs of mandibles of *Diplocheila polita* Dejean and *Dicrochile goryi* Boisduval. A–F, *Diplocheila polita*: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D and F, right mandible—dorsal, occlusal and ventral aspects, respectively. G–L, *Dicrochile goryi*: G, I and K, left mandible—dorsal, occlusal and ventral aspects, respectively; H, J and L, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: br, basal ridge; i, incisor; itr, inferior terebral ridge; prt, posterior retinacular tooth; rr, retinacular ridge; str, superior terebral ridge; tr, terebral ridge; tt, terebral tooth; vg, ventral groove; and vmt, ventral microtrichia. Scale bars = 200  $\mu$ m.

produce formic acid, and all but the Dicaelina produce hydrocarbons. Only the Dicrochilina produce aliphatic ketones. Absence of hydrocarbons and production of aliphatic ketones are regarded as apotypic features.

#### Characteristics of larvae

Within the Carabidae, licinine larvae are distinguishable by three features: head dorsally with frontal sutures extended posteriorly to the occipital suture; cervical

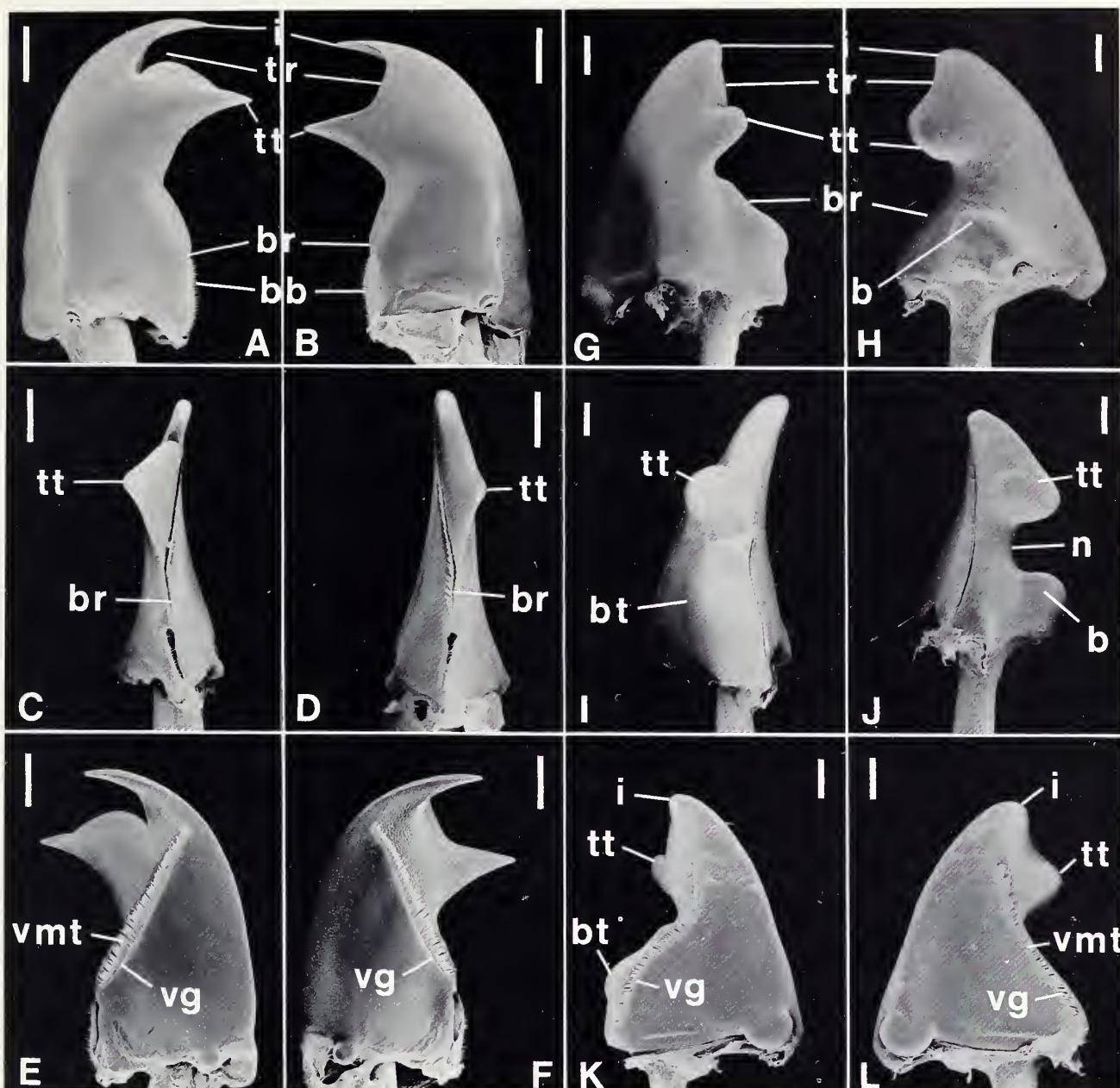


Fig. 3A–L. SEM photographs of mandibles of *Siagonyx* species? and *Licinus punctatulus* Fabricius. A–F, *Siagonyx* sp?: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D and F, right mandible—dorsal, occlusal and ventral aspects, respectively. G–L, *Licinus punctatulus*: G, I and K, left mandible—dorsal, occlusal and ventral aspects, respectively; H, J and L, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: b, dorsal boss; bb, basal brush; br, basal ridge; bt, basal tooth; i, incisor; n, notch in dorsal surface; tr, terebral ridge; tt, terebral tooth; vg, ventral groove; vmt, ventral microtrichia. Scale bars = 200  $\mu$ m.

suture forked, ventral apotome gula-like (Jeannel, 1942:989; Moore, 1966:160); antennae elongate, at least 1.5 $\times$  as long as mandibles (van Emden, 1942:44–45). Most known taxa have the occlusal margin of the terebra and posterior margin of the retinaculum denticulate or serrate (van Emden, 1942:44–45).

Although the tribe is diagnosed clearly by structural features of larvae, and although the few genera for which larval features are known (*Dicaelus*; *Diplocheila*; *Dicrochile*; *Siagonyx*; *Dilonchus*; *Licinus*; and *Badister*) are readily distinguished from one an-

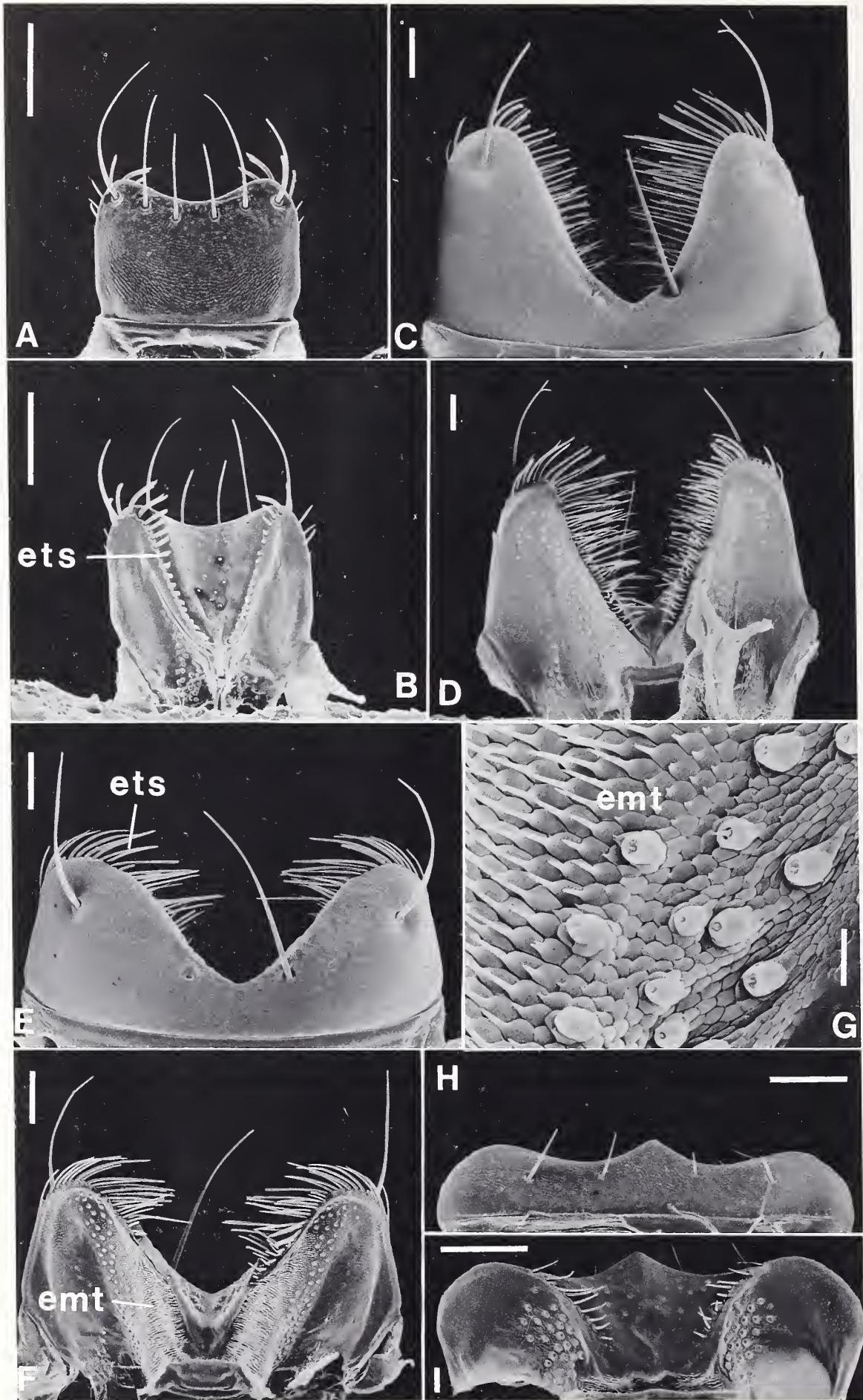


Fig. 4A–I. SEM photographs of the labrum of: *Loxandrus pactinillus* Allen (A–B); *Diplocheila daldorfi* Crotch (C–D); *D. polita* Dejean (E–G); and *Siagonyx* species? (H–I). A, C, E and H, dorsal aspects; B, D, F, G, and I, ventral aspects. Legend: emt, epipharyngeal microtrichia; ets, epipharyngeal trichoid sensilla. Scale bars = 200  $\mu$ m.

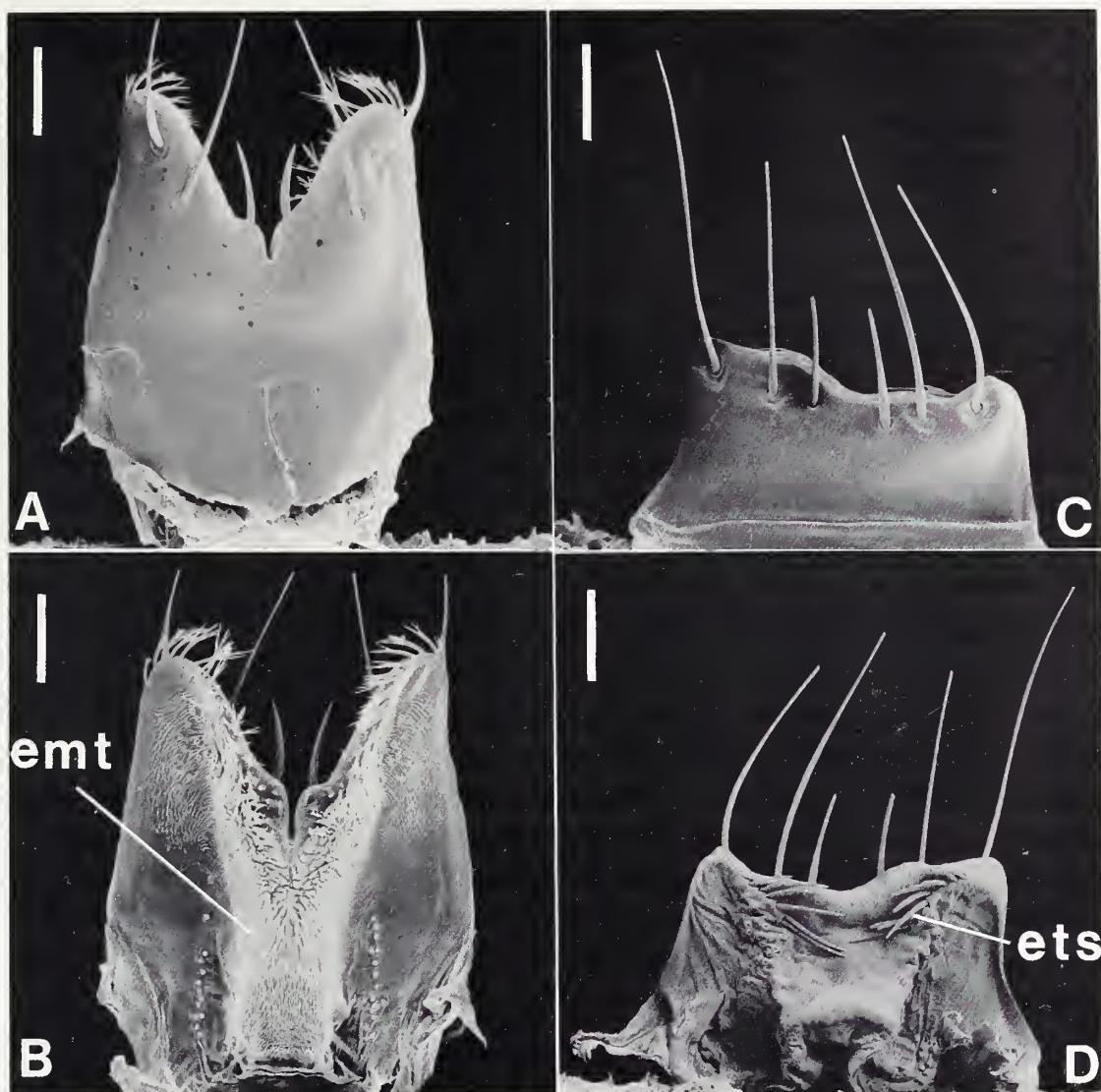


Fig. 5A–D. SEM photographs of the labrum of: *Dicrochile goryi* Boisduval (A–B); and *Licinus punctatulus* Fabricius (C–D). A and C, dorsal aspects; B and D, ventral aspects. Legend: emt, epipharyngeal microtrichia; ets, epipharyngeal trichoid sensilla. Scale bars = 200  $\mu\text{m}$ .

other, some groupings provided by these character states do not coincide with the subtribal limits based on adult features. For example, Jeannel (1942:990) grouped *Licinus* with *Dicaelus* in the Licinitae, and placed *Badister* by itself, in the Badisteritae. The smooth mandibles characteristic of *Diplocheila* larvae isolate this genus from all of the others, the latter exhibiting mandibles with serrate-edged terebrae and retinacula. In contrast, Moore (1966:160) noted that the larvae of *Lestignathus* and *Dicrochile* differed markedly from one another, and that such difference was in agreement with placing them in different groups of genera.

#### Chromosome numbers of Licinini

Serrano (1986:224) postulated 37 as a basic diploid chromosome number for Licinini and for “modern” groups of Carabidae generally (i.e., Harpalinae *sensu* Erwin, 1985). Numbers are as follows: for subtribe Dicaelina, represented by *Diplocheila* (three species), 37–42; and for subtribe Licinina, represented by *Badister anomalous* Perris, 45, and by *Licinus* (two species), 26 and 38 (Serrano and Yadav,

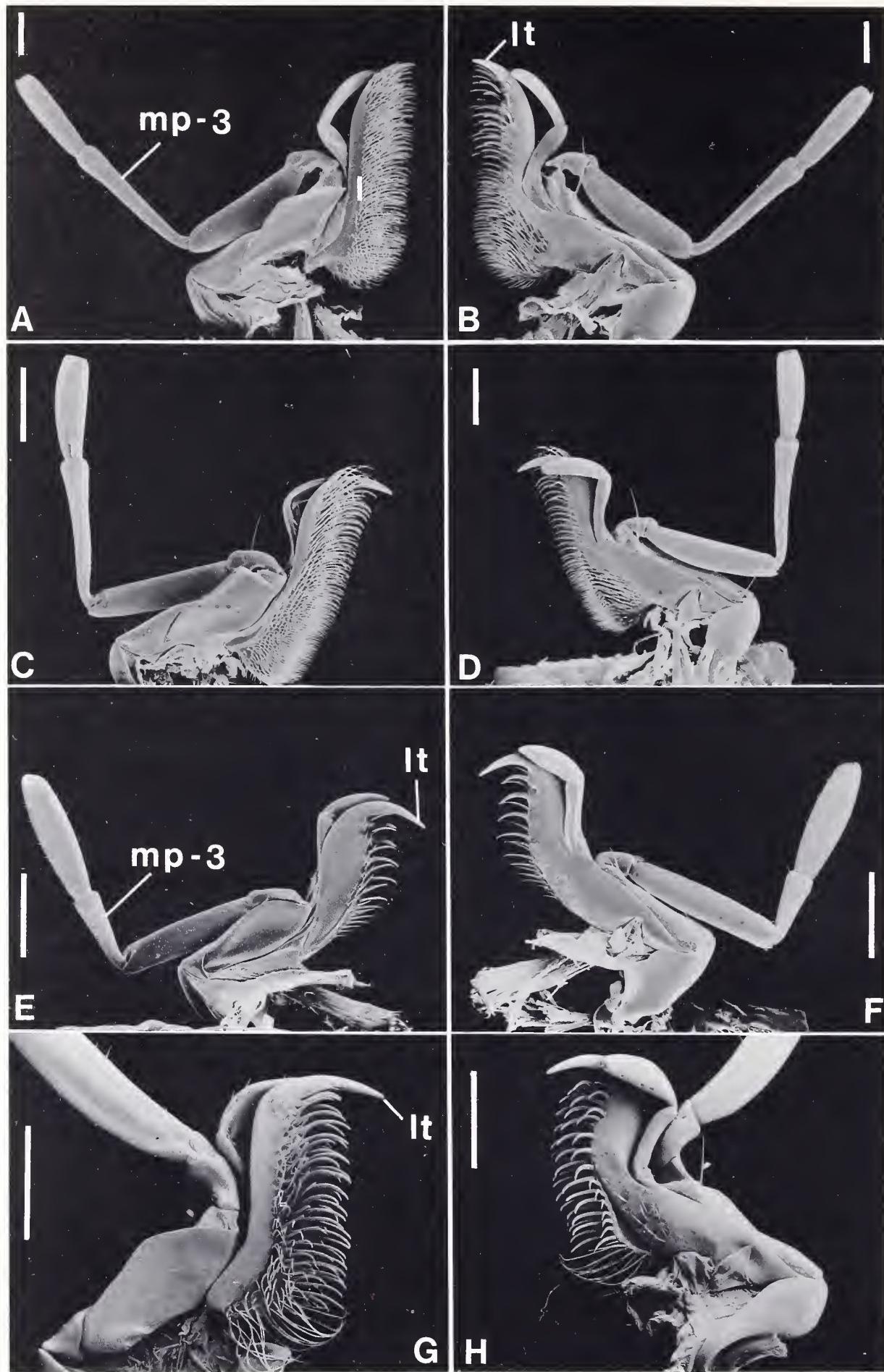


Fig. 6A–H. SEM photographs of the left maxilla of: *Diplocheila daldorfi* Crotch (A–B); *Diicrochile goryi* Boisduval (C–D); *Siagonyx* species (E–F); and *Licinus punctatulus* Fabricius (G–H). A, C, E and G, dorsal aspects; B, D, F and H, ventral aspects. Legend: 1, lacinia; lt, lacinial tooth; and mp-3, maxillary palpomere 3. Scale bars = 400  $\mu$ m.

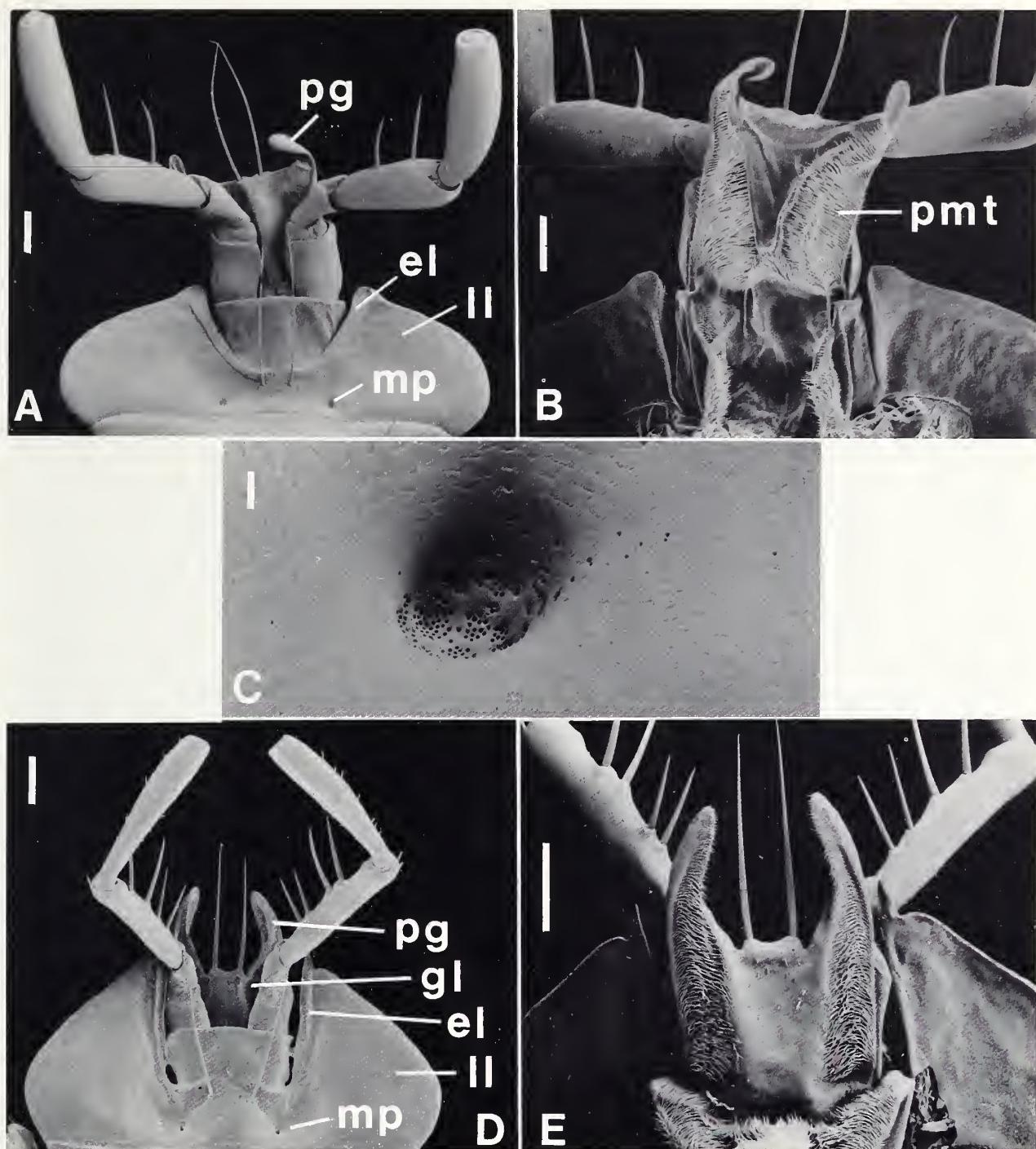


Fig. 7A–E. SEM photographs of the labium (mentum and prementum) of: *Diplocheila polita* Dejean (A–C); and *Dicrochile goryi* Boisduval (D–E). A, C and D, ventral aspects; B and E, dorsal aspects; C, enlargement of mental pit, showing pores. Legend: el, epilobe; gl, glossal sclerite; ll, lateral lobe; mp, mental pit; pg, paraglossa; and pmt, paraglossal microtrichia. Scale bars: A–B, D–E = 200  $\mu\text{m}$ ; C = 10  $\mu\text{m}$ .

1984:351; Serrano et al., 1986:134). These numbers indicate marked overlap at the subtribal and generic levels, and thus, they are of little use in suprageneric classification, except to confirm further the harpaloid affinities of the Licinini. Within genera, at the species level, chromosome number likely is useful. Serrano (1986:325) notes that, although similar in form and other structural features of adults, *Licinus aequatus* Serville ( $2N = 26$ ) and *L. punctatulus* Fabricius ( $2N = 38$ ) differ markedly

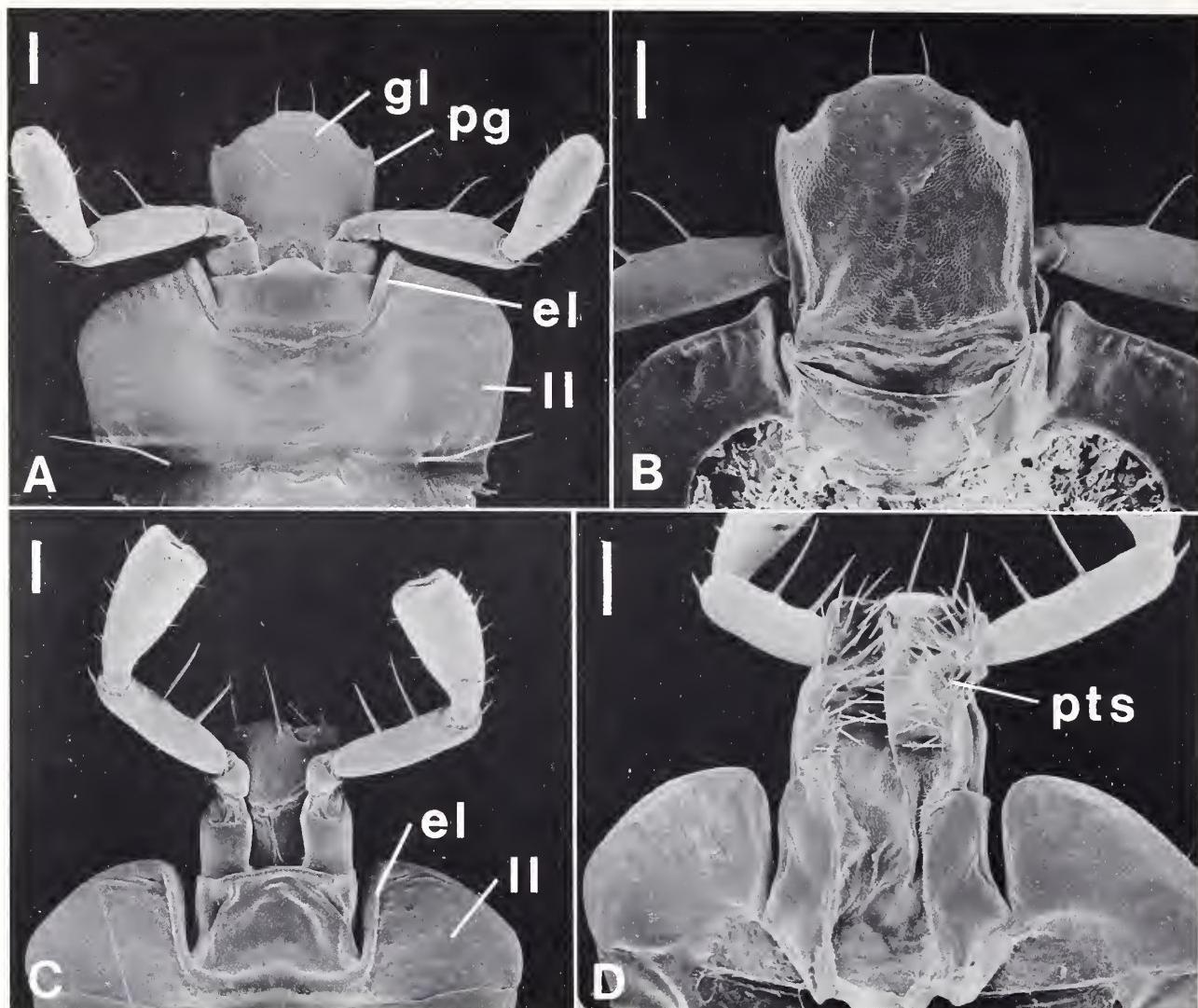


Fig. 8A-D. SEM photographs of the labium (mentum and prementum) of: *Siagonyx* species? (A-B); and *Licinus punctatulus* Fabricius (C-D). A and C, ventral aspects; B and D, dorsal aspects. Legend: el, epilobe; gl, glossal sclerite; ll, lateral lobe; pg, paraglossa; and pts, paraglossal trichoid sensilla. Scale bars = 200  $\mu$ m.

in chromosome number, indicating that karyotypic change has been more rapid than morphological change.

#### Food of Licinini

Lindroth (1986:403) reported that the larvae and probably also the adults of *Licinus depressus* Paykull ate snails. Harde (1984:106) reported that members of *Licinus hoffmannseggi* Panzer and unspecified species of *Badister* were molluscivores. Ball (1959:53) and Lindroth (1969:948) cited records of *Dicaelus purpuratus* Bonelli eating snails. I observed specimens of *Diplocheila oregonae* Hatch in captivity eating snails. To obtain the soft tissue, the beetles bit through the mollusc shells.

Mandibles of the lestignathines, with their long, slender incisors and terebral teeth, appear rather like those of cychrines (cf. Ball, 1966a:723, fig. 2A-B), which are known to prey on snails. However, rather than biting through the shell, a cychrine attacks the soft tissue by inserting its narrow head into the operculum. Perhaps lestignathines behave in the same manner.

Based on these few observations, I postulate that molluscivory is a general feature of licinines, and that such behavior is ancestral in this lineage.

### Monophyly of the tribe Licinini

Efforts have not been made previously to establish that the tribe Licinini is monophyletic. Ball (1959), for example, accepted implicitly the judgment of previous workers that the Licinini is a natural group, based primarily on modifications of the mouthparts, and principally the labrum and clypeus, with anterior margins of each more or less markedly excavated. As noted above, these features vary markedly within the Licinini. Other features of adults are likely not apotypic at the tribal level (number of supraorbital setae; adhesive vestiture of the fore tarsi; form of male genitalia) or are shared with other callistites (condition of the fore coxal cavities; mental pits). Larval features, such as long cerci (or urogomphi) and long antennae are shared variously with other callistites.

A few features of adults, reasonably interpreted as apotypic, characterize the Licinini and help to establish monophyly of the group: reduction of the length of the mandibular terebra relative to the basal area, absence of occlusal grooves, and an extensive ventral groove; and the labial mentum without a tooth and with the median sinus more extensive than usual (except in some lestignathines). Larval features that seem likely to be apotypic for the Licinini are: dorsal surface of the head with frontal sutures extended posteriorly to the occipital suture; and ventrally, with the cervical suture branched, isolating a median apotome. Additionally, I infer that molluscivory is a ground-plan feature, and is probably the driving selective force involved in modifications of the mandibles.

### Relationships of subtribes of Licinini

Within the Licinini, details of the mouthparts, especially the mandibles, seem to establish the monophyly of the Dicrochilina, Lestignathina, and Licinina. Additionally, within the Licinini, only the Dicrochilina have aliphatic ketones in their defensive secretions.

Evidence for monophyly of the Dicaelina, however, is less convincing. The larva of *Diplocheila*, for example, has a smooth, rather than serrate, terebral margin. This latter feature is characteristic of *Dicaelus* and the other groups of Licinini. The Dicaelina exhibit the most primitive mandibles (terebra relatively long, and various taxa with indications of remains of the retinaculum). Adults of *Dicaelus* lack hydrocarbons from their defensive secretions, producing formic acid only. Defensive secretions of *Diplocheila* have not been studied. If it is found that members of this genus also lack hydrocarbons, then this feature will serve as diagnostic for the Dicaelina.

At present then, the monophyly of the subtribe Dicaelina has not been established: either *Diplocheila* or *Dicaelus* may be more closely related to the derived subtribes than to one another. For example, the terebral margin and retinaculum of the mandibles of larvae of *Dicaelus* are serrate or denticulate, like those of known members of the other subtribes. In contrast, the larval mandibles of *Diplocheila* are smooth. If, as seems likely, the serrate mandibles are derived, then this feature could indicate that *Dicaelus* is related more closely to the other subtribes than to *Diplocheila*.

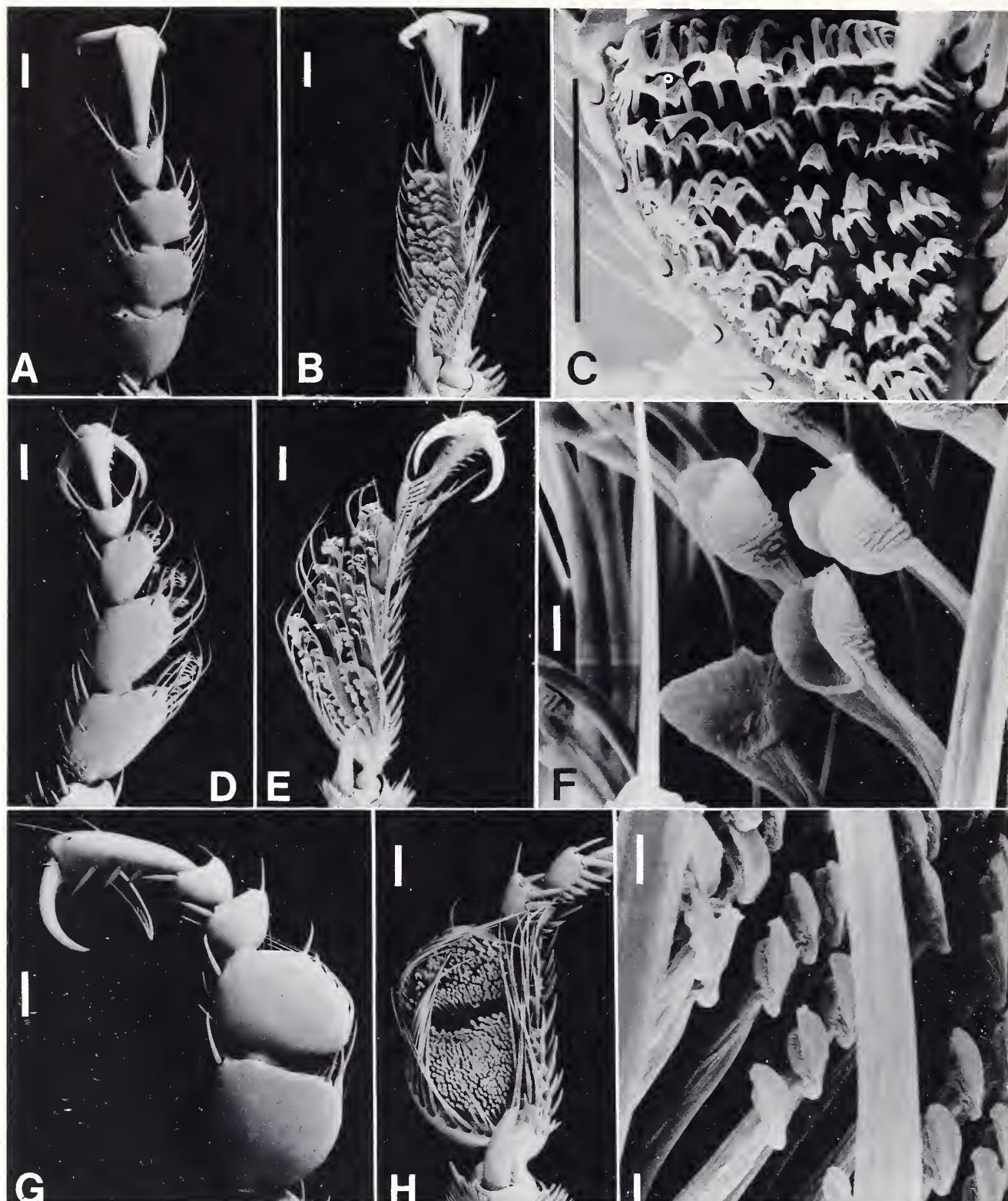


Fig. 9A-I. SEM photographs of left fore tarsus of males of: *Diplocheila polita* Dejean (A-C); *Dicrochile goryi* Boisduval (D-F); and *Licinus punctatulus* Fabricius (G-I). A, D and G, dorsal aspects; B, C, E, F, H and I, ventral aspects. Scale bars: A-E, G, H = 200  $\mu\text{m}$ ; F, I = 10  $\mu\text{m}$ .

However, until such relationship can be established firmly, it seems best to include these two genera in a single dibasic subtribe rather than recognizing two monobasic groups.

The markedly shortened terebra characteristic of the Dicrochilina, Lestignathina and Licinina is accepted as evidence for the monophyly of these three groups, which

collectively, I refer to as the derived assemblage. Within this assemblage, monophyly of the Dicrochilina and Lestignathina is postulated, on the basis of the biperforate coxal cavities exhibited by the members of this complex.

I believe, then, that the Dicaelina, if monophyletic, is the adelphotaxon of the derived assemblage of subtribes. Within the latter, the Dicrochilina and Lestignathina comprise a lineage that is the adelphotaxon of the Licinina. In summary, the subtribes of Licinini are related as follows: Dicaelina + ((Dicrochilina + Lestignathina) + Licinina).

**KEY TO SUBTRIBES, BASED ON FEATURES OF THE  
MOUTHPARTS OF ADULTS**

1. Mandibular terebra longer, about  $\frac{1}{2}$  length of mandible (Fig. 2A); terebral tooth small (Fig. 2A–B) or absent. Maxilla with lacinial tooth less prominent (Fig. 6A), occlusal margin densely setose; palpomere 3 longer than palpomere 4 (Fig. 6A–B, mp-3). Labium (Fig. 7A) with complete suture between submentum and mentum; mentum ventrally bisetose, paramedian pits (mp) near base of mentum, and palpomere 2 bisetose or quadrisetose ..... Subtribe Dicaelina
- 1'. Mandibular terebra smaller, about  $\frac{1}{3}$  length of mandible (Figs. 2G, 3A, G); terebral tooth various. Maxilla with lacinial tooth and proportions of maxillary palpomere 3 various. Labium with suture between mentum and submentum complete or not; mentum bisetose or asetose, with or without paramedian pits, and labial palpomere 2 bisetose or quadrisetose ..... 2
- 2.(1') Mandible with terebral tooth small (Fig. 2G–H, tt). Maxilla (Fig. 6C) with lacinial tooth (lt) moderately prominent, occlusal margin densely setose; maxillary palpomere 3 (mp-3) longer than palpomere 4. Labium (Fig. 7D) with complete suture between submentum and mentum; mentum bisetose, and with paramedian pits basally (mp); labial palpomere 2 quadrisetose ..... Subtribe Dicrochilina
- 2'. Mandible with terebral tooth prominent, either sharply pointed (Fig. 3A–B), or broad and blunt (Fig. 3G–H). Maxilla with lacinial tooth prominent, occlusal margin less densely setose (Fig. 6E–H), and maxillary palpomere 3 various. Labium suture between submentum and mentum complete or reduced; mentum bisetose or asetose, paramedian pits absent, and labial palpomere 2 bisetose ..... 3
- 3.(2') Mandibles about symmetrical, with incisor and terebral tooth long, slender, and pointed sharply (Fig. 3A–B). Maxilla with occlusal margin of lacinia sparsely setose (Fig. 6E–F); and maxillary palpomere 3 (mp-3) much shorter than 4. Labium with suture between submentum and mentum reduced or absent; mentum asetose, and medial sinus shallow (Fig. 8A) ..... Subtribe Lestignathina
- 3'. Mandibles markedly asymmetrical, either right or left with large basal boss (b) and deep notch (n) dorsally (Figs. 3G–H, 17B–C, 18D–E); terebral tooth broad and blunt (tt). Maxilla with occlusal margin of lacinia moderately setose (Fig. 6G–H); and maxillary palpomere 3 (mp-3) subequal in length to 4. Labium with suture between mentum and submentum complete; mentum bisetose, and medial sinus deep (Fig. 8C) ..... Subtribe Licinina

**Genus *Diplocheila* Brullé**

Ball (1959:11) arranged the species of *Diplocheila* in three subgenera: one monobasic, the Oriental *Neorembus* Ball; and two polybasic—the Oriental-eastern Pa-

laearctic *Diplocheila* (*sensu stricto*) and the widespread *Isorembus* Jeannel. Comments about the latter subgenera are as follows.

#### Subgenus *Diplocheila* (*sensu stricto*)

The species of this subgenus are difficult to distinguish from one another, especially using only external features of adults. More generally, these beetles resemble specimens of *Pterostichus* Bonelli. Probably such resemblance accounts for the following synonymy.

#### *Pterostichus (Platysma) karikali* Jedlička

Type material of *P. karikali* Jedlička, 1969 includes a holotype and 62 paratypes, in the ZSMM. The holotype is labelled: "S. Indien 1964/ Pondicherry State/ Karikal XI/ P. S. Nathan leg"; "Holotypus" [pink paper]; "Pterostichus/ karikali/ sp. n [handwritten]/ det. Ing. Jedlička" [pink paper]. Paratypes are from Karikal, also, and labels are similar to those associated with the holotype. All specimens in the type series are typical of *Diplocheila* (*sensu stricto*) *distinguenda* in the diagnostic features of that species (Ball, 1959:31, and fig. 59). Accordingly, I propose the new synonymy: *Pterostichus karikali* Jedlička, 1969 = *Diplocheila distinguenda* Laferté, 1851.

#### Subgenus *Isorembus* Jeannel

Ball (1959:48–49) organized the species of *Isorembus* in three groups: *zeelandica* group, with four species confined to the Oriental Region and eastern part of the Palaearctic Region; the *aegyptiaca* group, with three species that range collectively throughout the African continent and Madagascar, and on the southern edge of the Palaearctic Region eastward to Pakistan; and the *striatopunctata* group, confined to the Nearctic Region. Subsequently (Ball, 1966b:25), the southern Chinese species *Diplocheila minima* Jedlička (1931:103) was added to this species group. A formal reconstructed phylogeny is offered for the species groups, incorporating *D. minima* into the system that was proposed previously (Ball, 1959:91–94, and diagram 1). Comments about geographical history of the *striatopunctata* group are offered, below.

Reconstructed phylogeny.—See Figures 10 and 11. The basis for designation of character states as plesiomorphic or apomorphic is outgroup comparison, using as outgroups the genus *Dicaelus* and the hypothesized common ancestor of the subgenera *Diplocheila* (*sensu stricto*) and *Neorembus*. Ball (1959:91, lineage 14) lists ancestral states for *Isorembus* (Fig. 11, lineage V, here).

Figure 10 shows that few characters were available for reconstructing the phylogeny. It shows also that most of the changes were losses or reductions.

Evidence for group membership of *D. minima* was based originally on overall similarity (Ball, 1966b), although in fact two synapomorphies support this assignment, as is shown in Figure 10. In the 1966 paper, I stated mistakenly that the *aegyptiaca* group was characterized in part by a beaded (or margined) intercoxal process of the prosternum, a feature of the *striatopunctata* group and of *D. minima*. As indicated in Figure 10, the intercoxal process of members of the *aegyptiaca* group is unmargined. Absence of ensiform setae from the ovipositor stylomeres of females of the Nearctic species indicates that this geographically circumscribed assemblage is monophyletic.

## Geographical distribution and history

Ball (1959:96–98 and 1966b:22–25) discussed the geographical history of *Isorembus* against a geological background of continental stability, with the only possible terrestrial connection between Eurasia and North America being Beringia, in the north. More recently, it has become clear (and generally accepted by geologists) that continents have shifted in relation to one another, and that the disappearance of major epicontinental seaways has changed radically the configuration of land, and of sea basins (Noonan, 1988:40–43, and references cited therein).

Allen (1983), Noonan (1988) and Liebherr (1991a:137) have discussed the distribution patterns of various insect taxa (carabids and others) in the light of this geo-dynamic theory. It seems appropriate to extend such analysis to *Isorembus*, through correlation of the reconstructed phylogeny with past geological events (Liebherr, 1986:161).

The distribution pattern of *Isorembus* was illustrated by Ball (1966b:23, fig. 7), and it is tabulated in Figure 11. In more detail, the *aegyptiaca* group is marginal in the Oriental Region, being represented there by a single species in northern India, and *D. minima*, of the *striatopunctata* group is known only from Szechuan, in southern China—well to the west of the known range of the *zeelandica* group, which extends from the tropics of the Oriental Region to the cool temperate parts of the eastern Palaearctic Region. The ranges of the *zeelandica* and *aegyptiaca* groups are each more or less continuous.

In contrast, the range of the *striatopunctata* group is broadly interrupted, with a monophyletic assemblage of eight species in the Nearctic Region and a single species known only from Szechuan. Climatic tolerance of the Nearctic assemblage of the *striatopunctata* group extends from boreal conditions (two species) to the tropics (one species), with six species in the general area of cool to warm temperate conditions. To explain this pattern of geographical and ecological distribution, the following sequence of events is postulated.

1. Origin of *Isorembus* in Laurasia, probably in early Tertiary time, this stock becoming widespread, and occupying Euramerica, to the west of Turgai Straits, and southern Asiamerica in the east (Fig. 11, lineage V; see also Noonan, 1988: 42, fig. 3).
2. The eastern fragment of ancestral *Isorembus* differentiated into the ancestral stock of the *zeelandica* group (Fig. 11, lineage W), while the western fragment produced the ancestral stock of the *aegyptiaca-striatopunctata* groups (lineage X).
3. Separation of lineage X by an unknown vicariance event into a more southern stock (lineage Y), the ancestor of the *aegyptiaca* group, that eventually dispersed into the Afrotropical Region, and a more northern stock (lineage Z), the ancestor of the *striatopunctata* group.
4. Separation of the North American tectonic plate from Laurasia, with the consequent formation of the Atlantic Ocean basin, leading to division of lineage Z into the ancestor of the *D. minima* clade, and the ancestor of the extant Nearctic species of the *striatopunctata* group.
5. The Nearctic clade of the *striatopunctata* group, differentiated, and extending its overall climatic tolerance, entered the boreal forest, as the climate cooled in

later Tertiary time. Also, by overseas dispersal, one species extended its range to Cuba, in the West Indies.

6. The Palaearctic clade, meanwhile, extended its range across much of the temperate parts of the Palaearctic Region, but eventually became extinct over most of this area.

The large gap in the range of the *striatopunctata* group deserves additional comment. Although *Diplocheila minima* is isolated from the Nearctic clade of the *striatopunctata* group by thousands of kilometres, the extent of the terrestrial component of this separation may be comparatively recent. Based on fossil evidence, Coope (1979:264) noted that:

"In response to climatic oscillations of the Quaternary, species of Coleoptera have altered their geographic ranges on an enormous scale so that where a species is today may give us little evidence of its geographical history."

Two examples are offered in support of this statement, as follows. Coope (1973) reported that the aphodiine scarabaeid species *Aphodius holdereri* Reitter, known now from Tibet, only, was represented in Britain as recently as 26,000 years before present. Hammond et al. (1979) reported that the staphylinid species *Anotylus gibbulus* (Eppelsheim) known today only from eastern China and the Caspian Sea region, was present in Britain and eastern Canada during the Pleistocene, fossils having been collected in deposits ranging in age from ca. 39,000 to 300,000 years before present. Both of these species have undergone comparatively recent and dramatic range changes. It would seem possible, therefore, that the *Diplocheila striatopunctata* group was represented in Europe until the climatic changes of the Pleistocene epoch, with extensive subsequent extinction. Only *D. minima* survives, whose range may have extended far to the west of its present location, in southwestern China.

The main point of this discussion is that the distribution pattern of the *striatopunctata* group can be fitted very readily to the vicariance models proposed by Allen (1983) and Noonan (1988). Tempting as it is to propose a Jurassic origin for the *striatopunctata* group (cf. Allen, 1983:626, fig. 65), with postulated vicariance events paralleling so closely the reconstructed phylogeny of the *striatopunctata* group, it seems better to think in terms of a more recent origin and differentiation, and thus to postulate use of the warm temperate land connections across the North Atlantic Ocean in early Tertiary time (cf. Matthews, 1979:37, fig. 23). A Beringian route, postulated by Ball (1959, 1966b), seems less likely, in view of the present distribution pattern of the Nearctic clade, with its species concentration in the east and in warm temperate areas.

### New World species

Although Lindroth (1968:939) referred to Ball's (1959) revision of Licinini as having been done "with utmost accuracy," in fact I confused the names of two species of Nearctic *Diplocheila*: *D. modesta* Casey, 1920 is conspecific with *D. assimilis* LeConte, 1844, and the names therefore are synonymous; and *D. assimilis* Ball, 1959 (not LeConte) is conspecific with *D. impressicollis* Dejean, 1831. Lindroth (1968: 943–944) made the necessary corrections in the valid names for these species.

Table 2. Distribution pattern of the *Diplocheila striatopunctata* group in the Nearctic Region.

Species	Geographical zones					No. geog. zones
	East coastal states	Mid-west to 100th meridian	West of 100th to Rockies	West of Rockies		
<i>obtusa</i> LeC.	X	X	X	X		4
<i>striatopunctata</i> LeC.	X	X	X	X		4
<i>assimilis</i> LeC.	X	X				2
<i>impressicollis</i> Dej.	X	X				2
<i>major</i> LeC.	X	X				2
<i>oregona</i> Hatch			X	X		2
<i>undulata</i> Carr		X	X			2
<i>nupera</i> Casey	X					1
Total species	6	6	4	3		

*Diplocheila nupera* Casey

Locality record.—This rarely collected Floridian endemic, is known only from the southern half of that state (Ball, 1959:73). An additional record is:

Monroe County, Big Pine Key, Long Beach, June 21, 1990; three males, six females, collected by R. S. Anderson, from *Sesuvium* litter (CMNC).

The specimens were collected just above high tide line, by sifting debris consisting of parts of dead *Sesuvium* plants and material washed on land by the sea. Like most other members of this genus, adults of *D. minima* probably are hygrophilous, and on Big Pine Key, probably they live near the fresh water marshes that occur there (R. S. Anderson, pers. comm.). Thus, I believe that the sea beach record is accidental for this species.

*Diplocheila undulata* Carr

Locality record.—This rarely collected species is known from a few localities in Illinois, Manitoba, and Alberta. The species was described in 1920 on the basis of specimens labelled "Edmonton, Alberta" (Ball, 1959:8). Lindroth (1969:946) noted "Ecology not recorded for this species." Because its putative adelphotaxon, *D. obtusa* LeConte is unusual for *Isorembus*, living in mesic to dry situations, I assumed that *D. undulata* lived in similar habitats.

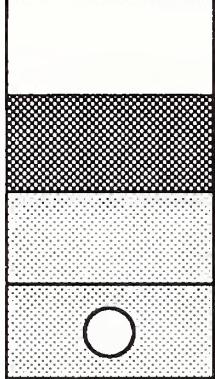
However, five specimens were collected in May and June, 1985, in pitfall traps placed at the edge of a permanent marl pond, and in adjacent sedge marsh, at Wagner Bog, which is located ca. 13 km west of Edmonton's city limits.

Technically, Wagner Bog is a mixed mire, with calcareous mud pools, and supporting a rich flora, including brown mosses and some *Sphagnum* (Vitt, 1982:17–22). Thus, *Diplocheila undulata* is hygrophilous, occupying a distinctive habitat. One of 60 species of carabids taken at Wagner Bog, *D. undulata* shares this area with many northern groups of ground beetles, such as *Blethisa*, *Elaphrus*, *Loricera*, *Patrobus*, *Agonum* (subgenus *Europhilus*), and *Chlaenius*.

CHAR. No.	CHARACTER	CHARACTER STATES AND TAXA			
		zeeland. group	aegypt. group	striatopunctata group <i>D. minima</i>	Nearctic spp.
7	♀ stylomere 2: setae number		(A)		(B)
6	Prosternum: apex				
5	Tarsomere 5: ventral setae				
4	Left mandible: basal occ. area				
3	Head: s-o setae number				
2	EI: interneur 1, base				
1	EI: discal seta				

LEGEND

Character State



(White square)	plesiotypic
(Diagonal hatching)	apotypic, gain
(Horizontal hatching)	apotypic, loss
(Circle)	apotypic, independent loss

Fig. 10. Characters and phylogenetic designation and distribution of character states among the species groups of subgenus *Isorembus* Jeannel.

#### Genus *Dicaelus* Bonelli

Ball (1959:102–103) arranged the 14 species of this genus recognized at that time into three subgenera: *Liodicaelus* Casey; *Paradicaelus* Ball; and *Dicaelus* (*sensu stricto*). Casual examination of additional material of *Paradicaelus* and subgenus *Dicaelus* that I have collected or received for identification has not revealed new taxa or any marked flaws in the classification that I proposed. Lindroth (1969:948) stated that he "... had nothing to add on the taxonomy of the genus," and confined his treatment to means of identification and characterization of the species of *Dicaelus* occurring in Canada.

Work in México during the past three decades produced new locality records and

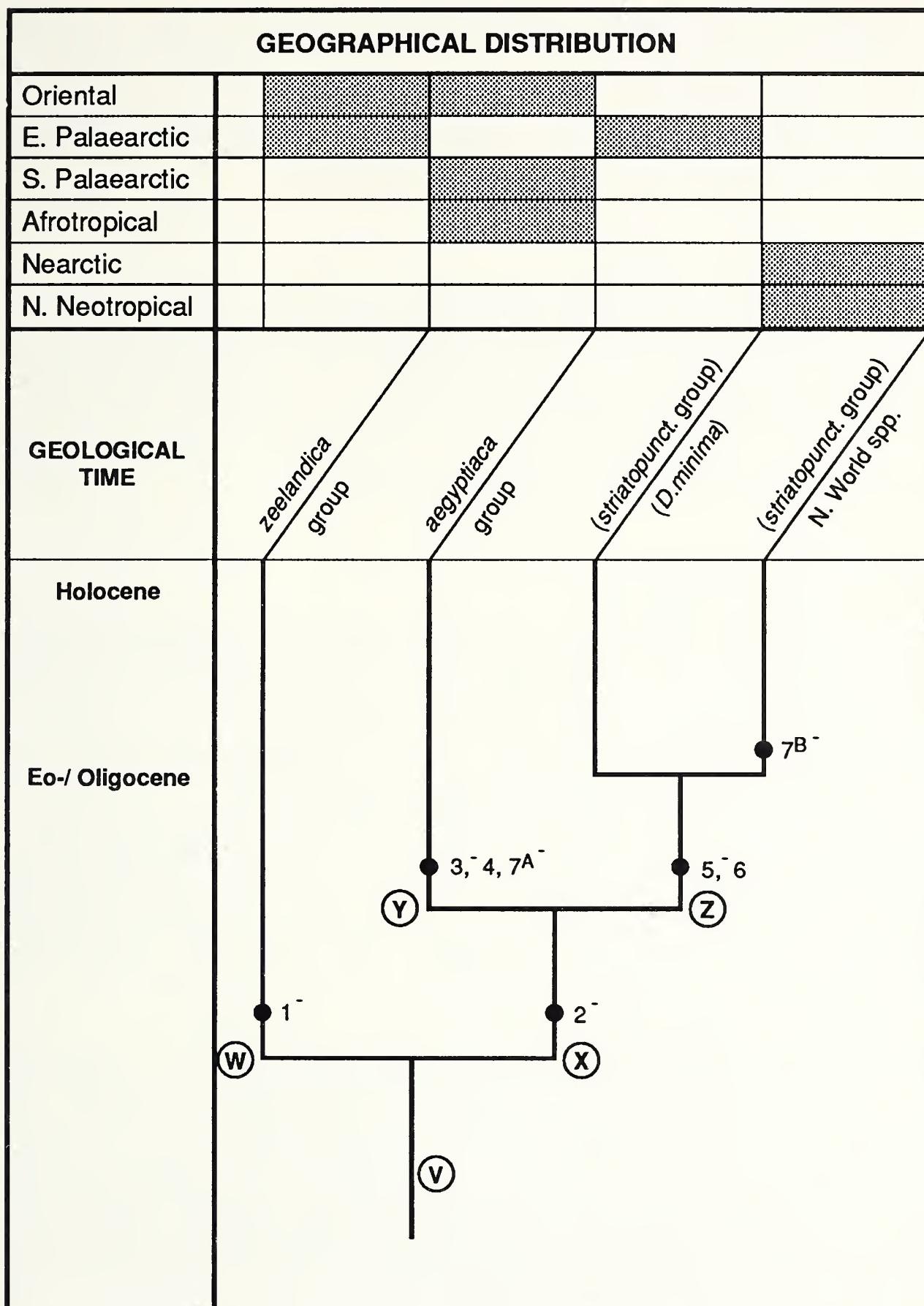


Fig. 11. Reconstructed phylogeny and geographical distribution of the species groups of subgenus *Isorembus* Jeannel.

a new species of *Liodicaelus*, as noted below. Also, the new material has led to modification of some previous decisions about ranking and recognition of taxa.

Because of the taxonomic importance of mandibles and diagnostic value of body proportions, these features are reviewed separately from the following descriptive treatment of taxa. A revised key to the species of *Liodicaelus* is provided, to accommodate the new species and taxonomic changes proposed.

### Subgenus *Liodicaelus* Casey

Figure 12 illustrates the habitus of a specimen of *Liodicaelus*. The most important feature for recognition is the nearly smooth elytra, resulting from absence of interneurs (or their reduction to rows of punctures), and flattening of the intervals. The subgenus is circumscribed geographically, being represented: only in the Great Plains States (and southern Alberta) west of the 100th meridian; in the southwest in New Mexico and Arizona; and in the mountains of México southward to the Trans-Volcanic Sierra (Figs. 17 and 18). Habitats occupied are grassland and dry to mesic forest, ranging in altitude from near sea level to more than 2,000 m.

#### Structural features: mandibles

The mandibles of *Liodicaelus* are average for Dicaelina: retinacular and molar ridges, occlusal grooves, and basal brush absent; ventral grooves each with short microtrichia (Fig. 13F, vmt). The left mandible lacks a terebral tooth, or has a small one; the terebral tooth of the right mandible is prominent.

Mandibles of *D. abbreviatus* Bates (Fig. 13A–F).—Left mandible (Fig. 13A, C, E) with terebral tooth (Fig. 13A) blunt, hardly projected; basal ridge narrow, not widened. Right mandible (Fig. 13B, D, F) average for *Liodicaelus*.

Mandibles of *D. laevipennis* LeConte (Fig. 13G–L).—Left mandible (Fig. 13G, I, K) with terebral ridge (tr) and basal ridge (br) nearly continuous, terebral tooth (tt) very small, hardly projected; basal ridge (br) slightly convex, evenly curved, in ventral aspect hardly extended beyond tips of ventral microtrichia (Fig. 13K). Right mandible (Fig. 13H, J, L) with terebral tooth prominent.

Mandibles of *D. franclemonti*, new species (Fig. 14A–F).—Left mandible (Fig. 14A, C, E) with terebral ridge (tr) and basal ridge (br) in one continuous curve, terebral tooth not evident; basal ridge projected well beyond tips of ventral microtrichia (Fig. 14F, vmt), and thickened as blunt basal tooth (bt). Right mandible (Fig. 14B, D, F) average for *Liodicaelus*: terebral tooth (tt) blunt and somewhat worn.

Comparisons.—These mandibles form a transformation series, from *D. abbreviatus*, with the best developed terebra, including tooth, to *D. franclemonti*, with terebra reduced and basal area enlarged. However, this sequence cannot be the complete basis for a reconstructed phylogeny, as indicated below (see notes about phylogenetic relationships, for *D. franclemonti*).

#### Structural features: measurements and body proportions

Tables 3–6 provide quantitative data about variation in size (length) and in proportions. For *Liodicaelus*, most such differences are not useful for distinguishing all

Table 3. Variation in Standardized Body Length (mm) among males and females of species and subspecies of subgenus *Liodicaelus* Casey.

Species and population sample	Males			Females		
	N	Range	Mean	N	Range	Mean
<i>D. franclemonti</i> , n. sp.						
Alazanas, Coahuila	1	14.9				
Cerro Potosi, N.L.	1	16.2		1	16.8	
<i>D. suffusus</i> Casey						
1959 data	6	13.4–14.8	14.3	6	12.1–15.5	14.4
Tres Rios (Son.), Chih.	5	11.1–12.2	11.7	3	12.0–12.4	12.3
vic. Col. Garcia, Chih.	7	12.3–13.2	12.8	6	13.1–13.3	13.2
vic. Madera, Chihuahua					12.7–13.6	13.1
vic. Tomochic, Chih.	7	12.9–14.3	13.5	5	12.8–13.9	13.3
<i>D. abbreviatus</i> Bates						
1959 data	1	15.2		3	15.3–15.6	15.4
W Huejuquillo el Alto Jal.	1	14.9				
W El Vergel, Durango	1	14.5				
<i>D. l. laevipennis</i> LeConte						
1959 data ( <i>l. laev.</i> )	16	16.5–20.0	18.8	9	17.2–19.0	18.4
1959 data ( <i>l. dicael.</i> )	3	17.0–17.6	17.3	11	17.1–19.1	18.0
Pinos Altos Mtns., N.M.	14	13.4–15.6	14.7	8	14.1–15.7	14.9
Col. Zaragosa, Chih.				1	17.2	
vic. Madera, Chihuahua	1	18.1				
<i>D. l. flohri</i> Bates						
1959 data	2	18.7–20.5	19.6	1	19.2	
Atlacomulco, México	3	16.2–16.8	16.5			
El Temascal, Durango	3	15.3–17.9	16.3	10	16.2–18.7	17.7
<i>D. chermocki</i> Ball						
1959 data				7	17.8–20.0	18.8
Huachuca Mtns., Arizona	2	17.2–18.3	17.8			

individuals of any one species from all other species, but they show trends, which may be employed in analysis of relationships.

Figure 15 is a scattergram on which are plotted values for the ratios PL/PWA and EL/EW. Because I do not have the original data summarized in the 1959 paper (tables 46, 47, 49), I have plotted only the mean values for these samples.

The position on the graph for each species is explained in simple terms, as follows. Points for *Dicaelus suffusus* occupy a central area, indicating pronota not especially narrowed apically, and elytra that are relatively narrow.

The points for both *D. chermocki* and *D. franclemonti* are low and more or less central on the graph, indicating broad pronota apically (to accommodate an enlarged head—cf. Fig. 12), and elytra of average proportions.

The points for *D. abbreviatus* occupy the left side of the graph, indicating short, broad elytra and pronotal apices that vary from broad to relatively narrow.

Table 4. Variation in values for the ratio PW/HW among males and females of species and subspecies of subgenus *Liodicaelus* Casey.

Species and population sample	Males			Females		
	N	Range	Mean	N	Range	Mean
<i>D. franclemonti</i> , n. sp.						
Alazanas, Coahuila	1	1.67				
Cerro Potosi, N.L.	1	1.64		1	1.63	
<i>D. suffusus</i> Casey						
1959 data	6	1.75–2.00	1.87	6	1.73–1.84	1.78
Tres Rios (Son.), Chih.	5	1.72–1.90	1.79	3	1.66–1.77	1.70
vic. Col. Garcia, Chih.	7	1.70–1.87	1.77	6	1.80–1.88	1.84
vic. Madera, Chihuahua				3	1.84–1.88	1.85
vic. Tomochic, Chih.	7	1.78–1.91	1.84	5	1.86–1.88	1.87
<i>D. abbreviatus</i> Bates						
1959 data	1	2.10		3	1.97–2.06	2.01
W Huejuquillo el Alto Jal.	1	1.94				
W El Vergel, Durango	1	2.06				
<i>D. l. laevipennis</i> LeConte						
1959 data ( <i>l. laev.</i> )	16	1.99–2.20	2.10	9	1.94–2.20	2.09
1959 data ( <i>l. dicael.</i> )	3	2.00–2.09	2.04	11	1.92–2.10	2.02
Pinos Altos Mtns., N.M.	14	1.86–2.09	1.97	8	1.88–2.03	1.97
Col. Zaragosa, Chih.				1	1.90	
vic. Madera, Chihuahua	1	2.07				
<i>D. l. flohri</i> Bates						
1959 data	2	2.06		1	2.12	
Atlacmulco, México	3	1.95–2.00	1.98			
El Temascal, Durango	3	2.03–2.17	2.11	10	1.98–2.20	2.08
<i>D. chermocki</i> Ball						
1959 data				7	1.53–1.71	1.62
Huachuca Mtns., Arizona	2	1.56–1.68	1.62			

The points for *D. laevipennis* are relatively high on the graph, indicating average elytral proportions but narrowed pronotal apices.

Overall, something of a radial pattern is indicated, with the center represented by *D. suffusus*, and outliers in different directions being: *D. chermocki* and *D. franclemonti*; *D. abbreviatus*; and *D. laevipennis*. No doubt, this pattern will be of use in phylogenetic analysis, although I doubt that the similarity exhibited by *D. chermocki* and *D. franclemonti* indicate close relationship of these taxa.

**KEY TO SPECIES AND SUBSPECIES OF SUBGENUS *LIODICAELUS*  
CASEY (MODIFIED FROM BALL, 1959:169)**

1. Elytral interval 7 not carinate. Elytra relatively short and broad, EL/EW 1.30–1.36  
..... *D. abbreviatus* Bates

Table 5. Variation in values for the ratio PL/PWA among males and females of species and subspecies of subgenus *Liodicaelus* Casey.

Species and population sample	Males			Females		
	N	Range	Mean	N	Range	Mean
<i>D. franclemonti</i> , n. sp.						
Alazanas, Coahuila	1	1.00				
Cerro Potosi, N.L.	1	0.98		1	0.95	
<i>D. suffusus</i> Casey						
1959 data	6	1.19–1.23	1.20	6	1.10–1.21	1.16
Tres Rios (Son.), Chih.	5	1.12–1.20	1.16	3	1.09–1.15	1.13
vic. Col. Garcia, Chih.	7	1.08–1.18	1.14	6	1.11–1.17	1.14
vic. Madera, Chihuahua				3	1.08–1.14	1.11
vic. Tomochic, Chih.	7	1.10–1.18	1.15	5	1.08–1.14	1.11
<i>D. abbreviatus</i> Bates						
1959 data	1	1.20		3	1.11–1.22	1.17
W Huejuquillo el Alto Jal.	1	1.07				
W El Vergel, Durango	1	1.24				
<i>D. l. laevipennis</i> LeConte						
1959 data ( <i>l. laev.</i> )	16	1.15–1.34	1.23	9	1.18–1.26	1.21
1959 data ( <i>l. dicael.</i> )	3	1.25–1.28	1.26	11	1.15–1.22	1.18
Pinos Altos Mtns., N.M.	14	1.18–1.29	1.24	8	1.15–1.30	1.21
Col. Zaragoza, Chih.				1	1.15	
vic. Madera, Chihuahua	1	1.25				
<i>D. l. flohri</i> Bates						
1959 data	2	1.24–1.30	1.27	1	1.24	
Atlacomulco, México	3	1.16–1.28	1.23			
El Temascal, Durango	3	1.14–1.21	1.17	10	1.13–1.21	1.17
<i>D. chermocki</i> Ball						
1959 data				7	0.98–1.05	1.00
Huachuca Mtns., Arizona	2	1.02–1.08	1.05			

- 1'. Elytral interval 7 carinate near humerus (cf. Fig. 12). Elytra of most specimens longer and more slender, EL/EW 1.34–1.52 ..... 2
- 2(1'). Head relatively large, PW/HW 1.53–1.71, and apical margin of pronotum relatively broad, PL/PWA 0.95–1.08 (cf. Fig. 12) ..... 3
- 2'. Head smaller, PW/HW 1.66–2.17 and apical margin of pronotum relatively narrow, PL/PWA 1.08–1.34 ..... 4
- 3(2). Elytral interneurs each a row of clearly impressed punctures. Range—mountains of southwestern Arizona ..... *D. chermocki* Ball
- 3'. Elytral interneurs impunctate, each a very shallow indistinct stria, or elytra smooth, without indication of interneurs (Fig. 12). Range—mountains of Sierra Madre Oriental, México ..... *D. franclemonti*, new species
- 4(2'). Size smaller, Standardized Body Length less than 15 mm (most specimens 12–14 mm). Pronotum anteriorly relatively broader (PL/PWA 1.23 or less) *D. suffusus* Casey
- 4'. Size larger, SBL 13 mm or more (most specimens 15–18 mm). Pronotum anteriorly relatively narrower (most specimens with PL/PWA more than 1.20; cf. Fig. 15) ... 5

Table 6. Variation in values for the ratio EL/EW among males and females of species and subspecies of subgenus *Liodicaelus* Casey.

Species and population sample	Males			Females		
	N	Range	Mean	N	Range	Mean
<i>D. franclemonti</i> , n. sp.						
Alazanas, Coahuila	1	1.44				
Cerro Potosi, N.L.	1	1.46		1	1.47	
<i>D. suffusus</i> Casey						
1959 data	6	1.46–1.52	1.50	6	1.44–1.55	1.48
Tres Rios (Son.), Chih.	5	1.41–1.50	1.45	3	1.41	1.41
vic. Col. Garcia, Chih.	7	1.40–1.50	1.46	6	1.36–1.46	1.40
vic. Madera, Chihuahua				3	1.38–1.43	1.40
vic. Tomochic, Chih.	7	1.36–1.42		5	1.33–1.41	1.38
<i>D. abbreviatus</i> Bates						
1959 data	1	1.33		3	1.30–1.36	1.32
W Huejuquillo el Alto Jal.	1	1.29				
W El Vergel, Durango	1	1.34				
<i>D. l. laevipennis</i> LeConte						
1959 data ( <i>l. laev.</i> )	16	1.42–1.55	1.48	9	1.40–1.50	1.44
1959 data ( <i>l. dicael.</i> )	3	1.45–1.48	1.46	11	1.40–1.54	1.44
Pinos Altos Mtns., N.M.	14	1.34–1.46	1.39	8	1.34–1.44	1.39
Col. Zaragosa, Chih.				1	1.39	
vic. Madera, Chihuahua	1	1.42				
<i>D. l. flohri</i> Bates						
1959 data	2	1.50–1.52	1.51	1	1.46	
Atlacomulco, México	3	1.40–1.43	1.42			
El Temascal, Durango	3	1.35–1.37	1.36	10	1.31–1.40	1.35
<i>D. chermocki</i> Ball						
1959 data				7	1.45–1.52	1.48
Huachuca Mtns., Arizona	2	1.34–1.41	1.38			

- 5(4'). Elytra with each interneur indicated by row of distinct punctures. Range—Chihuahua and Sonora, north to southern Alberta ..... *D. l. laevipennis* LeConte  
 5'. Elytra with interneurs 1–3 each indicated by row of distinct punctures; interneurs 4–8 either not evident, or punctures of interneurs 4–6 small, indistinct. Range—southern Durango, in the Sierra Madre Occidental, south to the state of México, in the Trans-Volcanic Sierra ..... *D. laevipennis flohri* Bates

THE SPECIES OF *LIODICAELUS*: NOTES,  
DESCRIPTIONS, AND DISTRIBUTION RECORDS

***Dicaelus (Liodicaelus) franclemonti*, new species**

Type material.—HOLOTYPE male, labelled: “MEX. Nuevo Leon/ Cerro de Potosi/ 12.4 mi. n.w./ Galeana, 7200'/ e. slope/ X.17.65”; “George E. Ball/ D. R. Whitehead/ collectors” (USNM). ALLOTYPIC female, labelled same as holotype



Fig. 12. Photograph of allotype of *Dicaelus (Liodicaelus) franclemonti*, new species, illustrating habitus. SBL = 16.8 mm.

(USNM). One additional PARATYPE, labelled: "MEX. Coahuila/ 21 km. e. San/ Antonio de las Alazanas 2550 m/ oak-madroño/ fir forest/ July 25, 1975"; "MEX EXP. 1975/ G. E. Ball & H. E. Frania/ collectors" (UASM).

Type locality.—México, state of Nuevo Leon, the mountain Cerro Potosí, northwest of Galeana.

Derivation of specific epithet.—Based on the surname of John G. Franclemont; this species is named in his honor, to commemorate on his 80th birthday his dedication to entomology and to the education of systematic entomologists.

Recognition.—Adults of this species share the following unique combination of character states: integument black, elytra virtually smooth, with traces only of smooth, impunctate interneurs (Fig. 12); head and apical margin of pronotum relatively broad. Males have a dorso-preapical projection on the median lobe, and the internal sac has four spines, only.

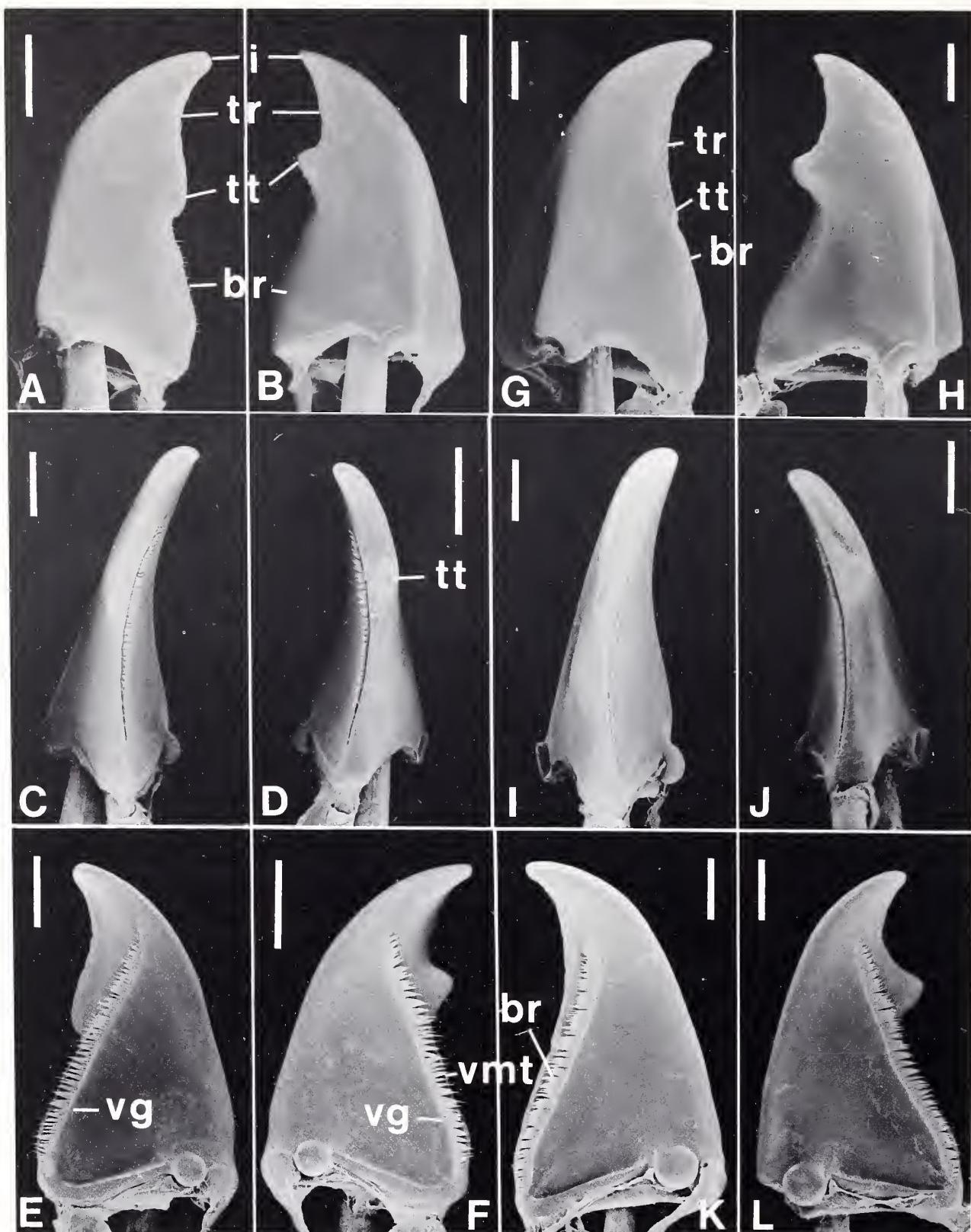


Fig. 13A–L. SEM photographs of the mandibles of *Dicelus abbreviatus* Bates and of *D. laevipennis* LeConte. A–F, *D. abbreviatus*: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D and F, right mandible—dorsal, occlusal and ventral aspects, respectively. G–L, *D. laevipennis*: G, I and K, left mandible—dorsal, occlusal and ventral aspects, respectively; H, J and L, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: br, basal ridge; i, incisor; tr, terebral ridge; tt, terebral tooth; vg, ventral groove; and vmt, ventral microtrichia. Scale bars = 400  $\mu\text{m}$ .

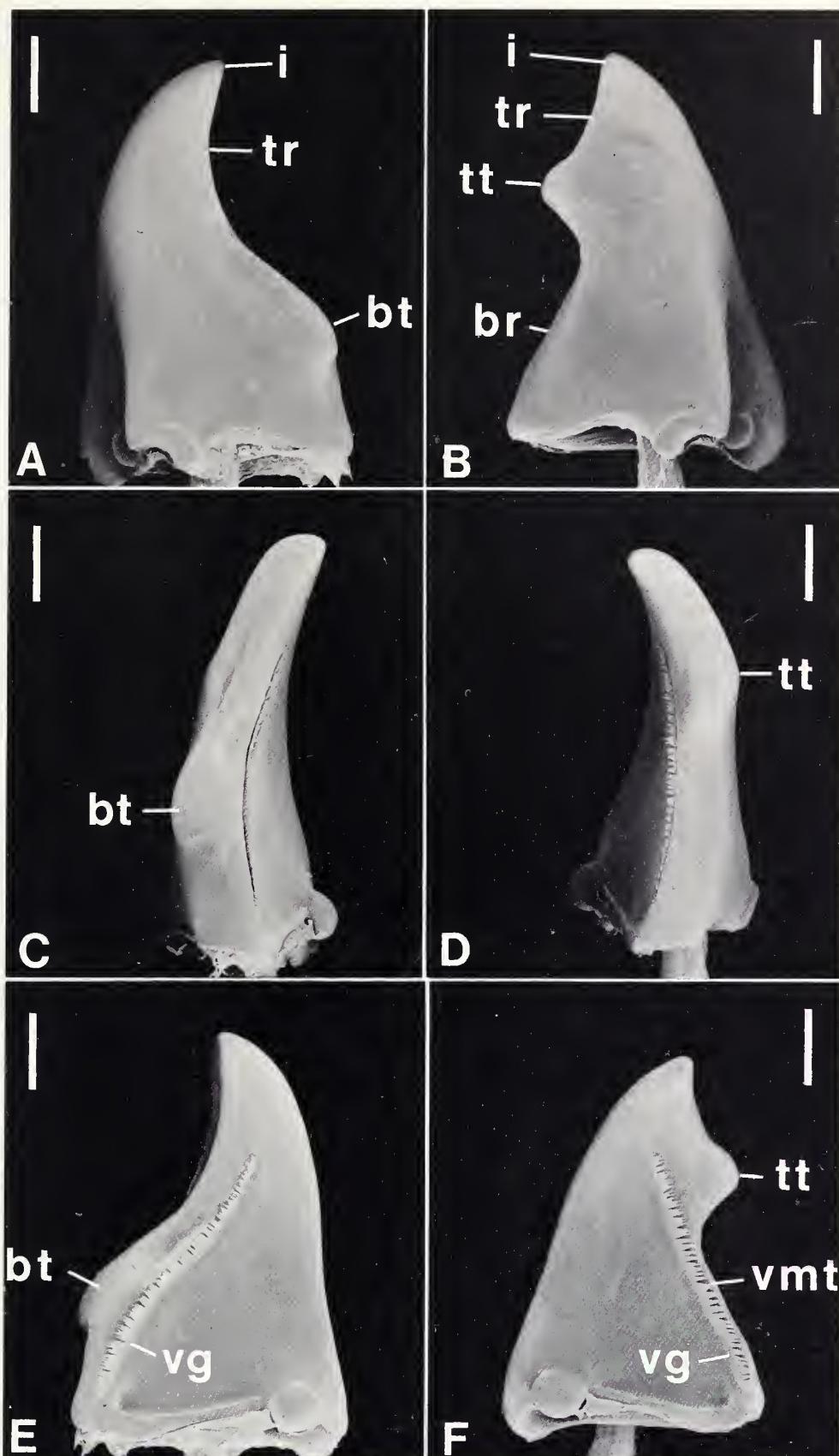


Fig. 14A-F. SEM photographs of the mandibles of *Dicaelus franclemonti*, new species: A, C and E, left mandible—dorsal, occlusal and ventral aspects, respectively; B, D and F, right mandible—dorsal, occlusal and ventral aspects, respectively. Legend: br, basal ridge; bt, basal tooth; i, incisor; tr, terebral ridge; tt, terebral tooth; vg, ventral groove; and vmt, ventral microtrichia. Scale bars = 400  $\mu\text{m}$ .

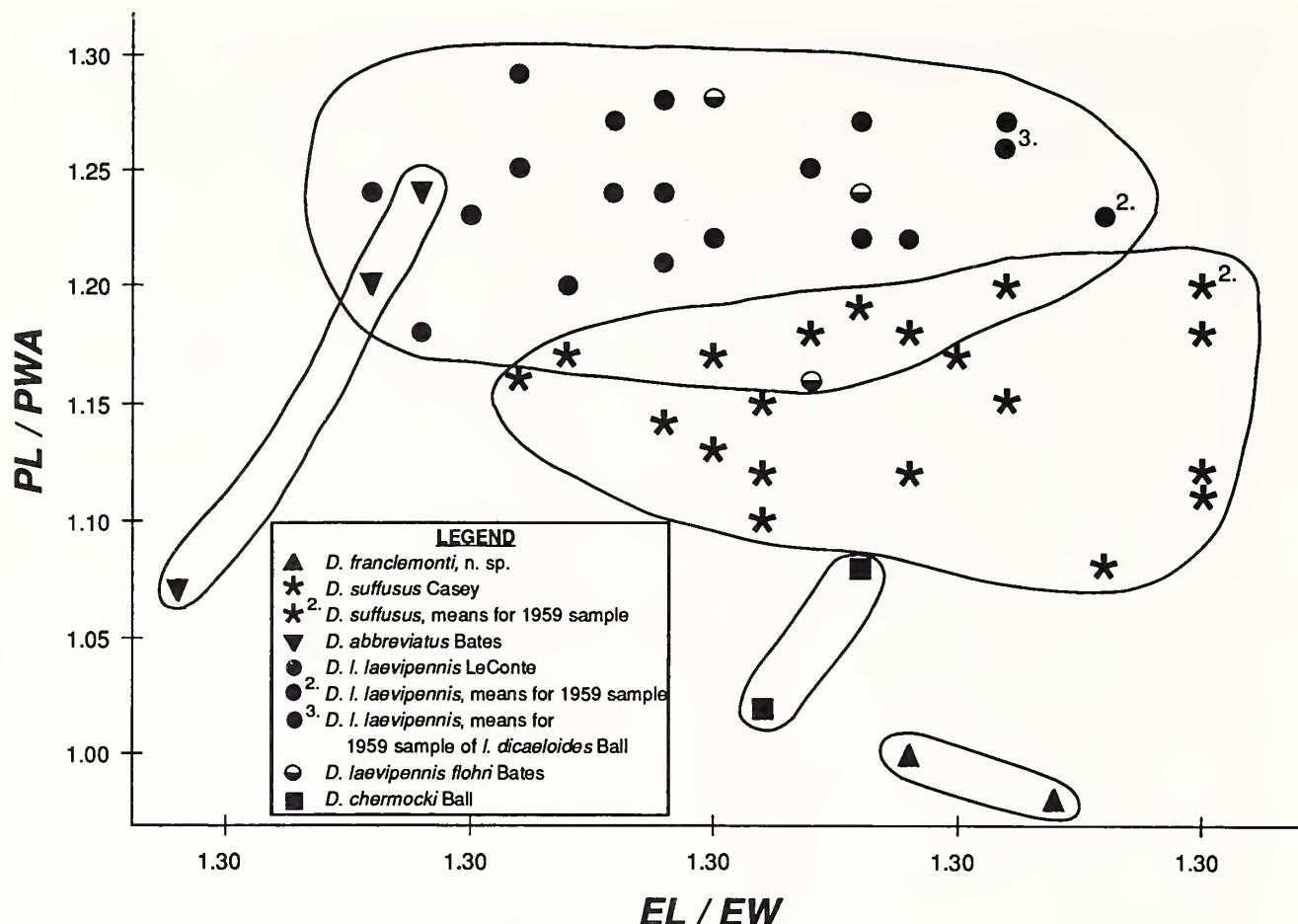


Fig. 15. Scattergram for ratios PL/PWA and EL/EW for the species of subgenus *Liodicaelus* Casey.

In body proportions, adults of *D. franclemonti* are most like those of *D. chermocki*. Smooth elytra, with hardly distinguishable impunctate elytral interneurs, distinguish *D. franclemonti*. Reduced elytral interneurs are characteristic of *D. laevipennis flohri* and *D. abbreviatus*, but adults of these species have smaller heads and prothoraces with narrower anterior margins.

**Description.**—With the character states of subgenus *Liodicaelus*. Habitus as in Figure 12. Data about Standardized Body Length, elytral width, and ratios PW/HW, PL/PWA, and EL/EW are presented in Tables 3–6. Integument black generally, with palpomeres dark rufous-piceous. Microsculpture of body generally isodiametric, sculpticells small and on dorsal surface slightly convex. Dorsal surface with soft silky luster. Head and pronotum with surface features as for other species of *Liodicaelus* (cf. Ball, 1959:176). Mandibles as in Fig. 14A–F. Elytra each with interval 7 toward humerus carinate, each carina ca. 0.25 length of elytron, and broader basally than in the other carinate species of *Liodicaelus*; otherwise, dorsal surface virtually smooth, interneurs indicated by indistinct lines. Sternum VII with apical setae 4–5 in males, and 2–4 in females.

**Male genitalia.** As in Figure 16A, B. Median lobe in left lateral aspect with basal part bent obliquely quite markedly; shaft with ventral surface straight, apex acute (Fig. 16A); in ventral aspect (Fig. 16B), apical portion straight, not curved to right; apex obtusely and evenly rounded, not notched shallowly. Internal sac with four large spines, only. Parameres average (cf. Ball, 1959, fig. 112c, d).

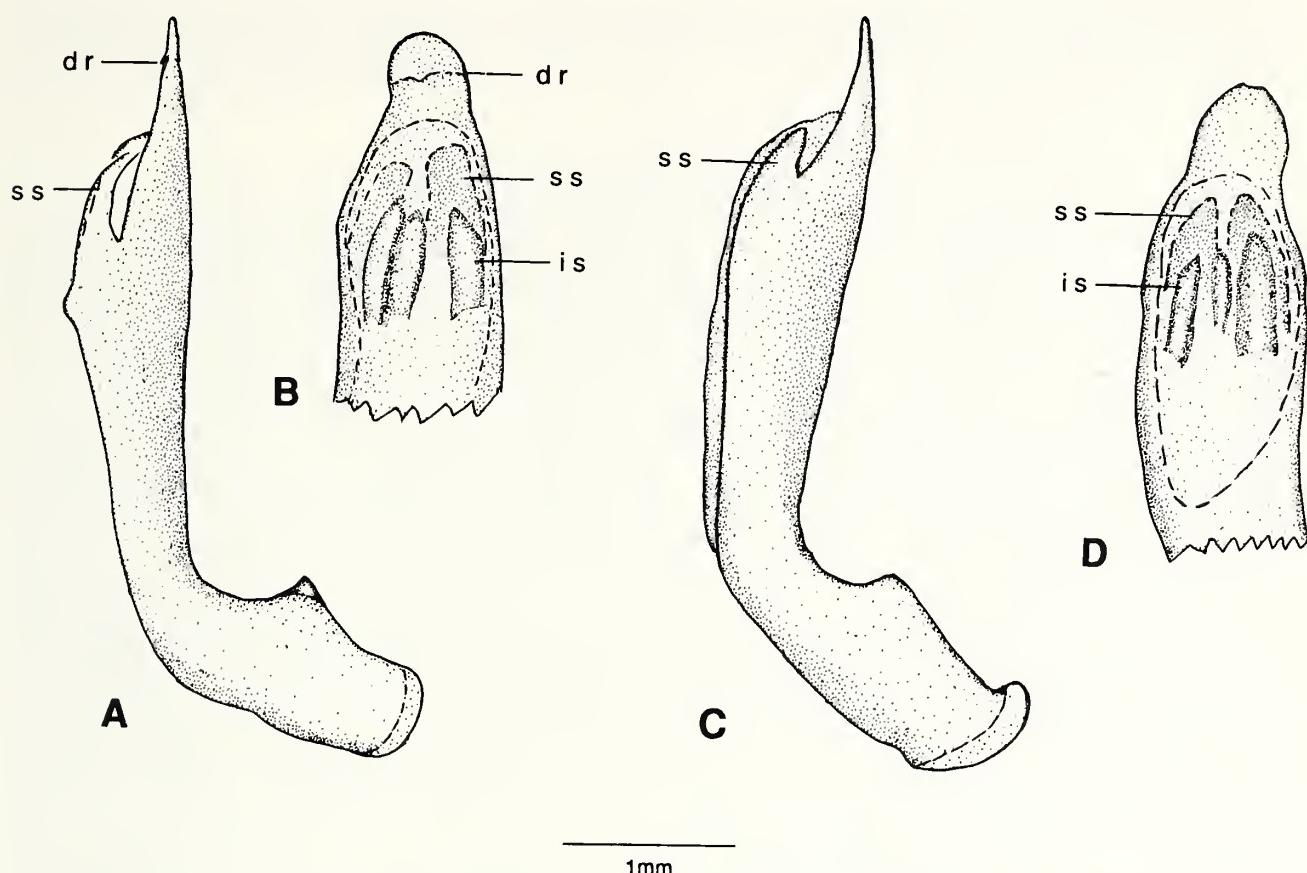


Fig. 16A-D. Line drawings of male genitalia of species of *Liodicaelus* Casey. A-B, median lobe of *D. franclemonti*, new species: A, median lobe, left lateral aspect; B, median lobe, apical portion, ventral aspect, showing armature of internal sac. C-D, median lobe of *D. chermocki* Ball: C, median lobe, left lateral aspect; and D, median lobe, apical portion, ventral aspect, showing armature of internal sac. Legend: dr, dorsal ridge; is, spine of internal sac; and ss, sclerotized strip.

**Habitat.**—On Cerro Potosí, the holotype and allotype of *D. franclemonti* were collected at an altitude of 2,200 m, in a damp stream bed, under stones, with a covering of oak and pine litter. The paratype male, collected near San Antonio de las Alazanas at 2,550 m, was under a log, in a dry conifer-oak forest. Therefore, I infer that *D. franclemonti* is an inhabitant of the mesic to dry montane forests that are characteristic of the upper slopes of the northern sierras, in México.

**Geographical distribution (Fig. 17).**—This species is known from the northern part of the Mexican Sierra Madre Oriental, only.

**Chorological affinities.**—*D. franclemonti* is isolated geographically from all other known species of *Dicaelus*. The other species of *Liodicaelus* occur to the north, in Texas (Fig. 18), or westward, in the Sierra Madre Occidental, or southward, in the Trans-Volcanic Sierra.

**Phylogenetic relationships.**—Based on features of the male genitalia, *D. franclemonti* is postulated to be the most primitive extant member of *Liodicaelus*, and to be the adelphotaxon of the other species of this subgenus. In turn, these species comprise a monophyletic assemblage, based on absence of the dorsal preapical ridge of the male median lobe, which is postulated to be a loss. This latter species assemblage is not analyzed further now, though the sequence of species used in the text

and summarized here indicates how I believe they are related, based on details of mandibular structure and body form: *D. suffusus-abbreviatus-laevipennis-chermocki*.

### *Dicaelus suffusus* Casey

This species was known previously from “the Sierra Madre Mountains of Chihuahua, Mexico” (type area) and from the Chiricahua Mountains of Arizona (Ball, 1959:177–178). Additional material documents more fully the range of *D. suffusus*.

Type locality.—Here restricted to the vicinity of Madera, Chihuahua, México.

Material examined.—Forty four specimens, from the following localities (Fig. 17).

U.S.A. ARIZONA. Cochise County. Female, Chiricahua Mts.: X.4.1937 Bryant Lot 65 (CASC). Male, Pinery Canyon, VII.9.1956; H. & A. Howden (CNCI). 2 females, Rustlers Park, 2,500 m, VII.14.1952, H. B. Leech, J. W. Green (CASC). 3 females, Rustlers Park, 2,560 m, VII.26–27.1979; A. Smetana (CNCI).

MÉXICO. CHIHUAHUA. 4 males, 4.8 km S Colonia Garcia, pine-oak-madroño forest, 2,130 m, VIII.4&28.1980; G. E. Ball, D. Shpeley, & W. Fraga (UASM). Male, 4 females, Colonia Garcia, meadow & adj. pine-oak forest, 2,130 m, VIII.5&28.1980; Ball, Shpeley & Fraga (UASM). 24 km E Creel, meadow, 2,200 m, VIII.24.1980; Ball, Shpeley & Fraga (UASM). Male, 2 females, 1.3 km NE Ejido Zaragosa, pine-oak forest, 1,850 m, VII.22.1979; J. S. Ashe, Ball & Shpeley (UASM). Male, ca. 14.8 km. E Ejido Zaragosa, pine-oak-aspen forest, 2,120 m, VIII.3.1980; Ball, Shpeley & Fraga (UASM). 2 females, 8.8 km W Madera, 2,270 m, VIII.30.1974; Ball & H. E. Frania (UASM). One female, 10.5 km W Madera, 2,320 m, pine-oak forest, 2,320 m, VIII.29–30.1974 (UASM). 3 males, 28.3 km E Mesa de Tres Rios (Sonora), pine-oak forest, 2,160 m, VII.7.1983; Frania, R. Jaagumagi & Shpeley (UASM). 7 males, five females, 25.4 km N Tomochic, pine-oak forest, 2,250 m, VIII.25.1980; Ball, Shpeley & Fraga (UASM).

SONORA. Male, female, Sierra Huachinera, 32–34 km NE Nacori Chico, pine-oak forest, 1,950 m, VIII.6–7.1982; G. E. & K. E. Ball & S. McCleve (UASM). Female, Sierra Huachinera, 56 km NE Nacori Chico, pine-oak forest, 2,330 m, VIII.8.1982; Ball, Ball & McCleve (UASM). Male, female, 18.5 km E Mesa de Tres Rios, pine-oak forest, 2,440 m, VII.7.1983; Frania, Jaagumagi & Shpeley (UASM).

### *Dicaelus abbreviatus* Bates

Described originally as a variety of *D. laevipennis* LeConte (Bates, 1891:239), from Refugio, Durango, this taxon is ranked as a distinct species on the basis of consistency of its diagnostic features (including mandibles, Fig. 13A–F) over its fairly extensive geographical range, and though it has not been collected in the exact same places as any other taxa of *Liocaelus*, its range is partially overlapped by the range of *D. laevipennis flohri* Bates (Fig. 17). Thus, *D. abbreviatus* maintains its distinctiveness in parapatry, if not sympatry.

Material examined.—Four specimens from the following localities (Fig. 17).

MÉXICO. DURANGO. Female, 68 km W Durango, 2,438 m, VI.18.1971 (CNCI). Male, 4.8 km E El Salto, VI.21.1964 (CNCI). Male, 72.9 km W Huajuquillo el Alto (Jalisco), rd. to Jesus Maria (Nayarit), 2,540 m, VII.28.1985, H. E. Frania, D. Shpeley (UASM).

SINALOA. Male, 199.4 km W El Vergel (Chihuahua), 2,400 m, pine-oak-madroño litter, VII.16.1983 (UASM).

*Dicaelus laevipennis* LeConte

Ball (1959:169–175) recognized four geographical races of this species: *D. l. laevipennis*; *D. l. dicaeloides* Ball; *D. l. abbreviatus*, and *D. l. flohri* Bates. See above for taxonomic treatment of *D. abbreviatus*. The subspecies *D. l. dicaeloides* (type locality Cludcroft, Otero Co., New Mexico [Ball, 1959:172]) was based on primarily the mandibular features of the type material. Re-examination of part of the type series satisfies me that the differences between the mandibles of this named form and nominotypical *D. laevipennis* is the result of wear, and thus without taxonomic significance. Accordingly, these two forms are regarded as consubspecific, and the name *D. l. dicaeloides* is a junior subjective synonym of *D. l. laevipennis* (**new synonymy**).

The gap in geographical range between *D. l. laevipennis* and *D. l. flohri* (Figs. 17 and 18) is substantial, but I think it represents a collecting artifact, only.

Material examined.—Forty five specimens of *D. l. laevipennis* and 13 specimens of *D. l. flohri*, from the following localities.

*D. l. laevipennis* LeConte (Fig. 18)

U.S.A. ARIZONA. Apache County. Male, St. Michael's, VI.8.1971; D. Brzoska (SEMC). Cochise Co. Male, Hwy. 666, 2.6 km SE Interstate Hwy 10, VII.29.1985; D. Brzoska (SEMC). Coconino Co. Female, Hwy. 64, S Grand Canyon Nat. Park, VIII.31.1967; P. S. Bartholemew (CASC). Mojave Co. Male, Peach Springs, VIII.22.1967; S. McCleve (SMCC). Navajo Co. Male, Show Low, IX.5.1967, Bartholemew (CASC). County not determined. Female, White Mts; D. K. Duncan (CASC).

COLORADO. Fremont Co. Female, Phantom Canyon. IX.13.1964; B. H. Banta (CASC). Kiowa Co. Female, Arlington, VIII.16.1947; H. G. Rodeck (CASC). Routt Co. Male, Steamboat Springs, 2,073 m, VI.15.1945; Bryant Lot (CASC). Teller Co. Male, Manitou, VIII.21.1958; A. C. Cole (CNCI).

MONTANA. Gallatin Co. Male, Bozeman, V.18.1926 (CNCI).

NEW MEXICO. Bernalillo Co. Female, Albuquerque, IX.19.1965; P. S. Bartholemew (CASC). Grant Co. Male, Hwy. 61, 51.8 km E Beaverhead, 2,469 m, IX.13.1967; Ball, T. L. Erwin & R. E. Leech (UASM). 5 males, 4 females, 16.1 km NE Pinos Altos, IX.12.1967; Ball, Erwin, & Leech (UASM). Male, 2 females, Hwy. 25, 46.8 km NE Pinos Altos, 1,920 m, IX.13.1967; Ball, Erwin & Leech (UASM). Hidalgo Co. Female, 3.2 km NE Rodeo, VII.30.1963; A. Rathke (CNCI). Otero Co. Female, Lincoln Nat. Forest, 3.2 km NE Cludcroft, 2,530 m, VII.13.1969; A. Smetana (CNCI). Rio Arriba Co. Male, Capulin Mountain, IV.21.1951; Bryant Lot 5 (CASC). Socorro Co. Male, Magdalena Mountains, 32.2 km S Magdalena, 2,316 m, VIII.19.1969; G. E. & K. E. Ball (UASM).

SOUTH DAKOTA. Fall River Co. Female, Hot Springs, IX.19.1906; E. Van Sant (CASC).

MÉXICO. CHIHUAHUA. Female, 4.5–6.5 km N Ejido Zaragosa, dry pine-oak forest, under logs, 2,000 m, VII.23.1979; J. S. Ashe, G. E. Ball & D. Shpeley (UASM).

Male, Hwy. 16, 21 km SE Madera, 2,100 m, grassland, IX.1.1974; Frania & Ball (UASM).

*D. l. flohri* Bates (Fig. 17)

MÉXICO. DURANGO. 2 males, 11 females, Reserva de la Biosfera La Michilia, El Temascal meadow, Potrillo La Laguna, 5 km S Trampa Las Casas, VIII.19.1980; Ball, Shpeley & Fraga (UASM).

MÉXICO (state of). 3 males, 6.4 km N Atlacomulco, 2,652 m, VIII.15.1974; C. W. & L. O'Brien & B. Marshall (UASM).

ZACATECAS. Male, 1.9 km SW Villa de los . . . [?], 2,350 m, VIII.1966; D. Thompson (UASM).

*Dicaelus chermocki* Ball

The original description of this species was based on seven females, males being unknown at that time (Ball, 1959:177). Subsequently, males were collected, and the genitalia (Fig. 16C–D) were found to be identical to those of *D. laevipennis* and the other taxa recognized in 1959.

*Dicaelus chermocki* is known only from the Huachuca and Chiricahua Mountains of southeastern Arizona (Fig. 17). The few additional specimens collected since 1959 confirm the distinctness of the species, and extend its altitudinal range downward from 2,286 m in the Huachuca Mountains to 1,402 m, at Sierra Vista, which is located at the base of that mountain range.

Material examined.—Three specimens from the following localities (Fig. 17).

U.S.A. ARIZONA. Cochise County. Huachuca Mts.: male, Carr Cr., fir-pine forest, 2,150 m, VII.23.1976; Ball, J. M. Campbell & P. M. Hammond (UASM); male, Ramsey Cr., III.22.1956, F. G. Werner, G. D. Butler (UASM). Female, Sierra Vista, VII.29.1963, R. F. Sternitsky (CNCI).

**Notes about geographical history of *Liodicaelus***

Ball (1959:185) noted the general association of *Liodicaelus* with the Madro-Tertiary flora, but did not attempt a biogeographic analysis because the species were known from few localities, and thus their ranges were understood inadequately. The additional locality data presented above improves knowledge of the species ranges, and the new species provides a new perspective. Furthermore, Liebherr (1991a:137–150, 1991b) provided a valuable general vicariance-based model and geological time-frame for interpretation of distribution patterns of montane taxa in México and southwestern United States.

Briefly stated, Liebherr's analysis explains the geographical history of vicariously distributed taxa in terms of a sequence of range barriers operating in sequence:

1. isolation of the Trans-Volcanic Sierra (M) from the northern Sierra Madre Oriental (A') + northern Sierra Madre Occidental (A + B) + southeastern Arizona (A'') + the rest of North America (N.A.);
2. isolation of A' from (A + B) + A'' + N.A.;
3. isolation of (A + B) from A'' + N.A.;
4. isolation of A'' from N.A.

Table 7. Distribution pattern of the taxa of subgenus *Liodicaelus* Casey, in terms of vicariance areas of Liebherr (1991b).

Taxon	Areas <sup>1</sup>				
	M	A'	A + B	A''	N.A.
<i>franclemonti</i> , n. sp.		<u>X<sup>2</sup></u>			
<i>suffusus</i> Casey			X <sup>3</sup>	X	
<i>abbreviatus</i> Bates			<u>X</u>		
<i>l. laevipennis</i> LeC.			X <sup>3</sup>	X	X
<i>l. flohri</i> Bates	X		X <sup>4</sup>		
<i>chermocki</i> Ball				<u>X</u>	

<sup>1</sup> Areas: M, Trans-Volcanic Sierra; A', northern Sierra Madre Oriental; A + B, northern Sierra Madre Occidental; A'', southwestern U.S.A. (see text for details); and N.A., North America, north, west and east of A''.

<sup>2</sup> X, a species known from a single area, only.

<sup>3</sup> In the northern part of A + B, only.

<sup>4</sup> In the southernmost part, only.

The time span inferred for this sequence of events is ca. 12 million years, beginning in Late Miocene.

The species of *Liodicaelus* are placed, in Table 7, in the context of Liebherr's analysis. Four points emerge: first, each area has a taxon that is endemic or nearly endemic to it; second, although *D. abbreviatus* and *D. suffusus* are in the Sierra Madre Occidental, their ranges seem not to overlap; third, the northern Sierra Madre Oriental has in it a taxon that is postulated to be the most primitive member of the subgenus, and to be the adelphotaxon of the remaining taxa; and fourth, ignoring the gap that separates *D. l. laevipennis* from *D. l. flohri*, the total range of *D. laevipennis* bridges all of the vicariance areas, except for the Sierra Madre Oriental. Points one and two, regarding endemism, indicate that differentiation in *Liodicaelus* has been influenced by the same sets of barriers and conditions that have influenced differentiation of many other taxa in northern México. To this extent, the data for *Liodicaelus* fit the general geographical pattern described by Liebherr. However, concerning the phylogenetic pattern, the fit of the taxa of *Liodicaelus* is inexact (point three). One would expect the most primitive adelphotaxon, postulated to be *D. franclemonti*, to be in the Trans-Volcanic Sierra and perhaps the southern part of the Sierra Madre Occidental—i.e., in the area occupied by *D. l. flohri*. This element of discordance suggests that the sequence of vicariance events for *Liodicaelus* was different from the sequence indicated by Liebherr's interpretation of the data that he used.

Because of the extensive range overlap of *D. laevipennis* with the ranges of the other species, the distribution data suggest also that the barriers in the west, between the Trans-Volcanic Sierra, the northern Sierra Madre Occidental and the Rocky Mountain outliers in Arizona are more readily penetrated than the barrier between the Sierra Madre Oriental and the Sierra Madre Occidental. Indeed, in spite of the postulated Pleistocene connections between the eastern and western montane biotas, there is evidence to the contrary—for example the *Carabus forreri* (S. M. Occidental-

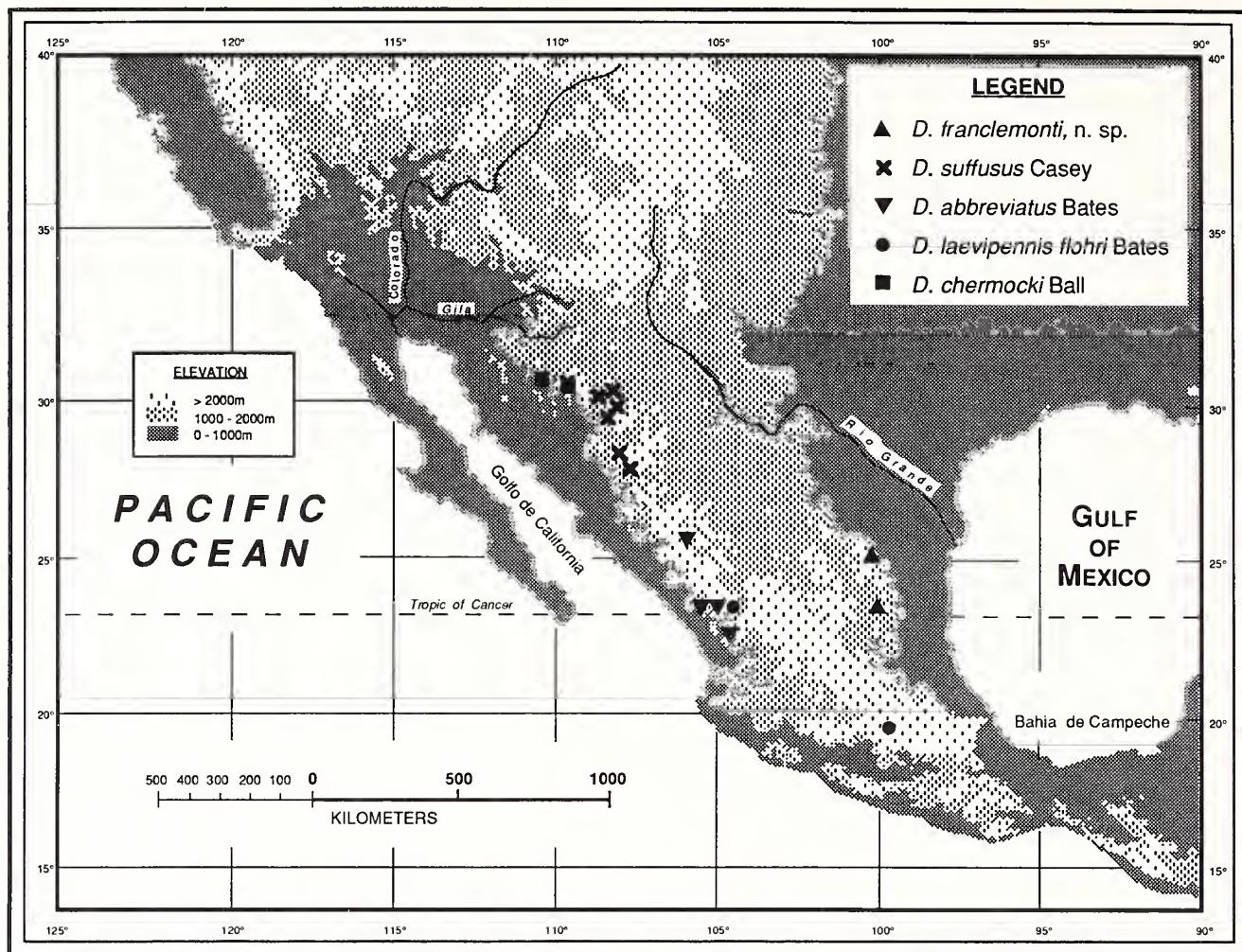


Fig. 17. Geographical distribution of the taxa of subgenus *Liodicaelus* Casey (except *D. l. laevipennis*) in México and southwestern United States.

southern Arizona)—*C. hendrichsi* (S. M. Oriental) species pair, absence of *Scaphinotus* from the Sierra Madre Oriental, and primitive species of subgenus *Progaleritina* Jeannel and of *Pasimachus* Bonelli isolated in the eastern Mexican forests from their western counterparts.

Nonetheless, I am disinclined to believe that a single general sequential pattern of taxon/area relationships exists, just as I am inclined to believe that barriers between adjacent mountain systems are permeable to semi-permeable as frequently as they are impermeable to taxa on either side of them. Probably different taxa, even with flightless adults and though they occupy similar habitats, differ in their tolerances to environmental conditions. Thus, what is an impermeable barrier to one taxon is crossed with difficulty by some others, and with ease by still others. Given a geographical situation such as one encounters in northern México and southwestern United States, one can expect to find a general concordance of taxon/area patterns, but not one that is precise.

Nonetheless, I am intrigued by and appreciate the elegance of Liebherr's analysis that is based on principles of cladistic biogeography. As well, I concede that a cladistic analysis of the taxa of *Liodicaelus* may, after all, support the pattern that he has postulated.

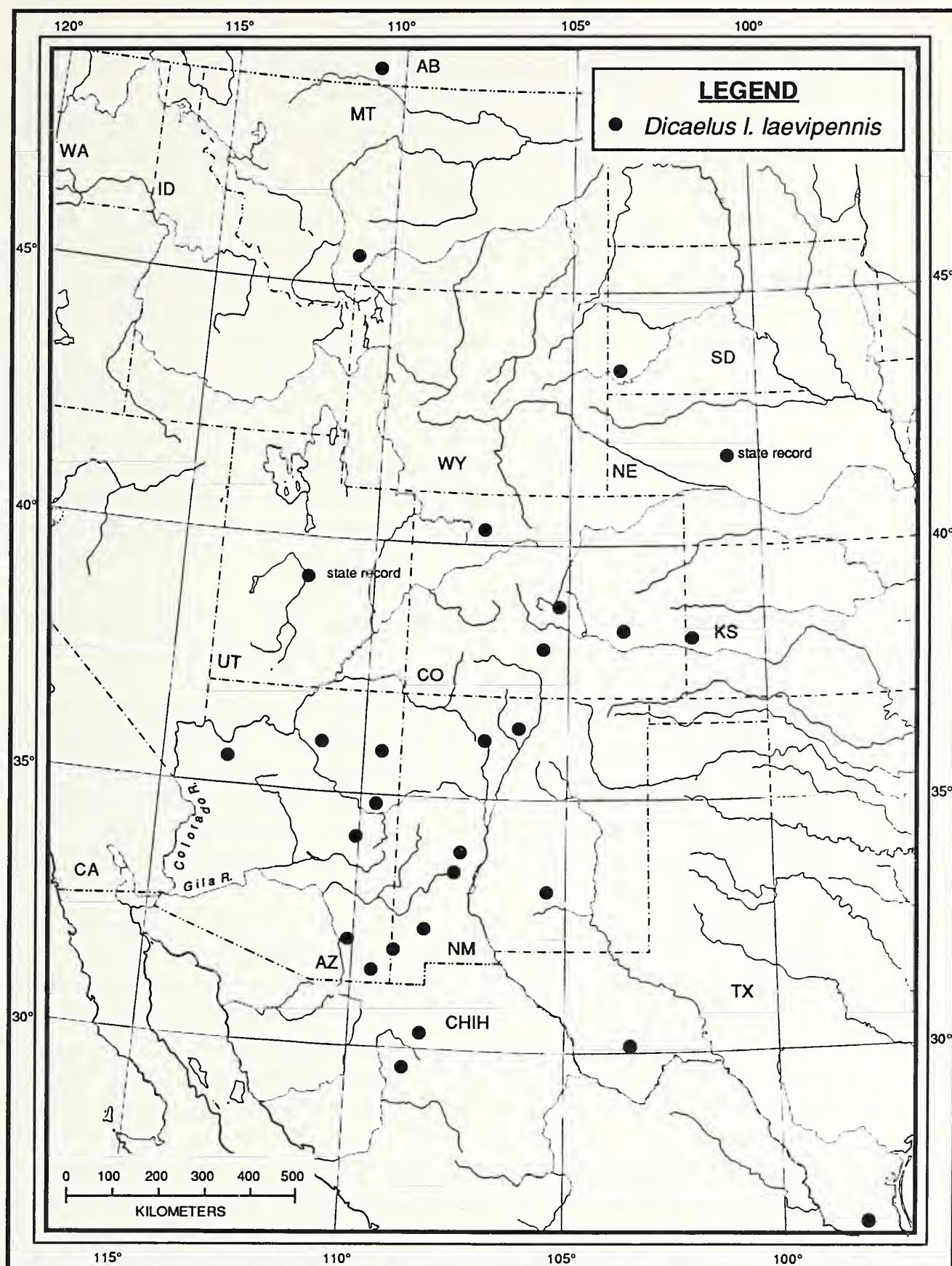


Fig. 18. Geographical distribution of *Dicaelus l. laevipennis* LeConte.

### Genus *Badister* Clairville

Specimens of *Badister* are rare in collections, primarily because they are small, rather inconspicuous, and most of them live in habitats so wet that they are avoided by most collectors. Nonetheless, I have seen many specimens during the past years, and identifying them has given sufficient opportunity to test the delimitation of taxa recognized in my treatment of the genus (Ball, 1959:191–241). Further, Lindroth (1969:955–967) confirmed implicitly my species-level treatment, though he differed with some of my interpretations of supraspecific relationships and classification. Such differences require comment, and some new information has become available that seems worthy of reporting, as detailed below. Also, I take this opportunity to offer a more detailed treatment of microsculpture for several species.

In classifying the North American species of *Badister* (Ball, 1959:190–191), I recognized three subgenera: *Badister* (*sensu stricto*), *Trimorphus* Stephens and *Baudia* Ragusa. These taxa were characterized primarily by details of mandibular structure and tarsal setation: right mandible with dorsal surface notched, and tarsomere 5 with a row of setae on each ventro-lateral margin (*Badister*); right mandible with dorsal surface notched, tarsomere 5 with ventro-lateral margins asetose (*Trimorphus*); and left mandible notched, tarsomere 5 with ventro-lateral margins asetose (*Baudia*). For classification of the species of subgenus *Badister*, I used the ranks of complex and group, as follows: *bipustulatus* complex—*bipustulatus* group (5 species), and *neopulchellus* group (5 species); *pulchellus* complex—*pulchellus* group (including *B. pulchellus* LeConte, only), and *elegans* group (5 species).

Lindroth (1969:955–967), who preferred not to use a formal subgeneric rank, recognized four species groups: *notatus* group, including only *B. notatus* Haldeman, that I included in subgenus *Badister*; the *pulchellus* group, for the other species of subgenus *Badister*; the *transversus* group, for the single Nearctic species (*B. transversus*) that I included in subgenus *Trimorphus*; and the *reflexus* group for most of the species of *Baudia*. He did not recognize formally any ranks between group and subgenus.

Lindroth's assignment of *B. notatus* to a group equal in rank to a subgenus, was based on the several striking features that are unique in the genus, such as reduction of microsculpture, reduction of wings and loss of ability to fly, and development of convex elytral intervals. However, *B. notatus* exhibits the derived feature of large spines in the internal sac, which is characteristic of the *elegans* group. Thus, Lindroth classified *B. notatus* on the basis of phenetic distinctness, whereas I classified it on the basis of what is interpreted to be a shared derived feature; in other words, I used phylogenetic principles.

Lindroth (1969:962) accepted my judgement that *B. transversus* was isolated from the other subgenera of *Badister*, but he did not agree that it was related to the type species of *Trimorphus* (*B. sodalis* Duftschmid), although both species are similar in mandibular notching, and both have tarsomere 5 asetose. Noting the similarity between members of *Baudia* and of *B. transversus* in reduced tarsal setation and transverse pronotal microsculpture, Lindroth (1969:956) implied that the latter species was a *Baudia* derivative, whose mandibles exhibited reverse asymmetry (i.e., the right mandible notched, rather than the left). He concluded the argument by suggesting that the difference in which one of the mandibles of a pair was notched was the result

Table 8. Notching of mandibles among West Indian population samples of *Badister reflexus* LeConte.

Island(s)	Notched mandible		Total
	Left	Right	
Bahamas	4	0	4
Cuba	4	2	6
Jamaica	2	0	2
Cayman Islands	1	10	11
Hispaniola			
Haiti	1	4	5
Dom. Republic	3	3	6
Total	15	19	34

of a very simple genetic difference. If this is so, mandibular notching cannot be regarded as a reliable character for grouping the species of *Badister*. This matter is addressed below, following description of the clypeus, labrum and mandibles of *Badister*.

#### Labrum, clypeus and mandibles of *Badister* (Figs. 19A-H and 20A-F)

The mouthparts of *Badister* adults are modified strikingly, particularly the labrum, clypeus and mandibles. The clypeus (Fig. 20A-B, cl) is narrow, sharply bent in a dorso-ventral plane, with two prominent lateral setae. The labrum (l) is deeply, angularly notched, with six marginal dorsal setae.

Structure of the mandibles (Figs. 19A-H, 20C-F).—This pair of sclerites is typical of the Licinina in being short and broad, lacking molar teeth, retinaculum and occlusal grooves. Strikingly asymmetrical, one of the pair has a deep dorsal notch (Figs. 19A, B, E, and 20E-F), and ventrally (Fig. 19G-H) the ventral groove of the notched mandible is markedly curved.

For the subgenus *Baudia* Ragusa, notching of the left mandible is normal (Fig. 19A-B, E-G, n) the notch being located between an anterior much enlarged terebral tooth (tt) and posterior basal boss (b). The occlusal margin in dorso-lateral aspect (Fig. 19B-G) is markedly bent. The right mandible (Fig. 19C, D, F, H) is without the deep dorsal notch, and without the basal boss. For the subgenus *Badister* (*sensu stricto*), the right mandible is notched (as in Fig. 20E-F), with enlarged terebral tooth and basal boss, and the left mandible is without notch or projections.

Most known species of *Badister* are constant in which mandible is notched—either right or left, but not both. The West Indian populations of *Badister reflexus* LeConte are exceptional, in that either mandible of a pair is notched, as illustrated in Figures 19 and 20. This species has been placed in the subgenus *Baudia* Ragusa (Ball, 1959: 221), a group characterized by having the left mandible notched.

Implications for classification.—The data for *Badister reflexus* seem to support Lindroth's opinion that the notching pattern of the mandibles is determined by a simple genetic change. I doubt that such a character by itself is likely to distinguish monophyletic lineages. Thus, it seems best either to abandon the subgenera as they

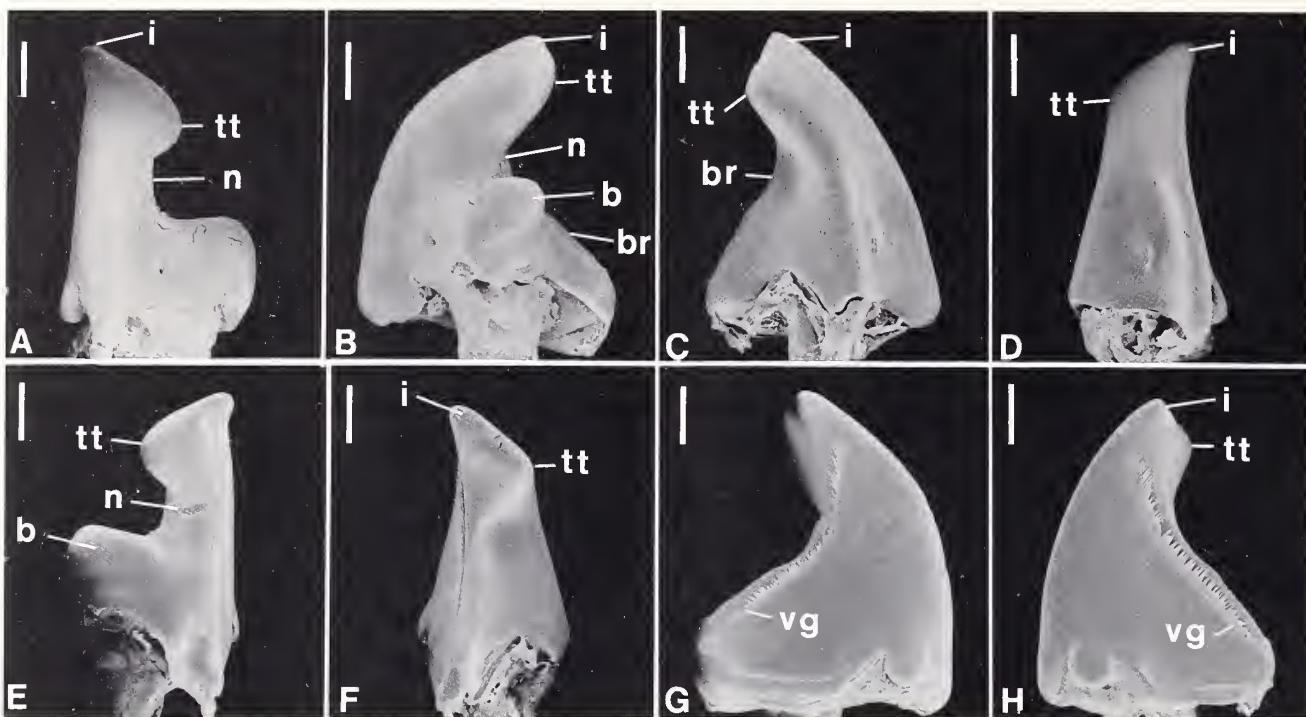


Fig. 19A–H. SEM photographs of the mandibles of *Badister reflexus* LeConte: A, B, E, and G, left mandible, lateral, dorsal, occlusal and ventral aspects, respectively; C, D, F and H, dorsal, lateral, occlusal, and ventral aspects, respectively. Legend: b, basal boss; br, basal ridge; i, incisor; n, notch in dorsal surface; tt, terebral tooth; and vg, ventral groove. Scale bars = 100  $\mu$ m.

are diagnosed at present, or to acknowledge that each is likely to be a polyphyletic assemblage and to use it because of tradition or convenience.

#### Microsculpture of *Badister* (Fig. 21A–H)

Elytral microsculpture in the *bipustulatus* complex.—Most species of *Badister* with which I am familiar either lack elytral microsculpture (*B. notatus* Haldeman) or have markedly transverse and closely packed meshes (*B. neopulchellus* Lindroth, Fig. 21A–B), with very narrow sculpticells (s), and an iridescent luster—a condition designated as “grated” by Allen and Ball (1980:486). An exception is *Badister obtusus* LeConte (Figs. 21C–D), with the mesh pattern slightly transverse, sculpticells wider, and surface rather dull—lacking iridescence. There is an ecological correlate to this difference: *B. neopulchellus* is markedly hygrophilous, whereas *B. notatus* and *B. obtusus* occupy the forest floor in damp to dry areas, but not in association with standing water.

It is accepted generally that isodiametric microsculpture (Fig. 21E–F) is plesiomorphic, and any other conditions are more or less apomorphic, in a transformation series, with the markedly transverse grated condition marking the far end. I had assumed that the series was essentially irreversible. If this were so, then *B. obtusus* should occupy a relatively primitive position. However, with *Badister obtusus* being part of a derived clade in a lineage nearly all members of which exhibit grated microsculpture (Ball, 1959:233, Diagram 3), it seems unlikely that this species can be regarded as ancestral to the lineage as a whole. Accordingly, I conclude that the non-grated microsculpture exhibited by *B. obtusus* is derived from the grated condition, and that this derivation

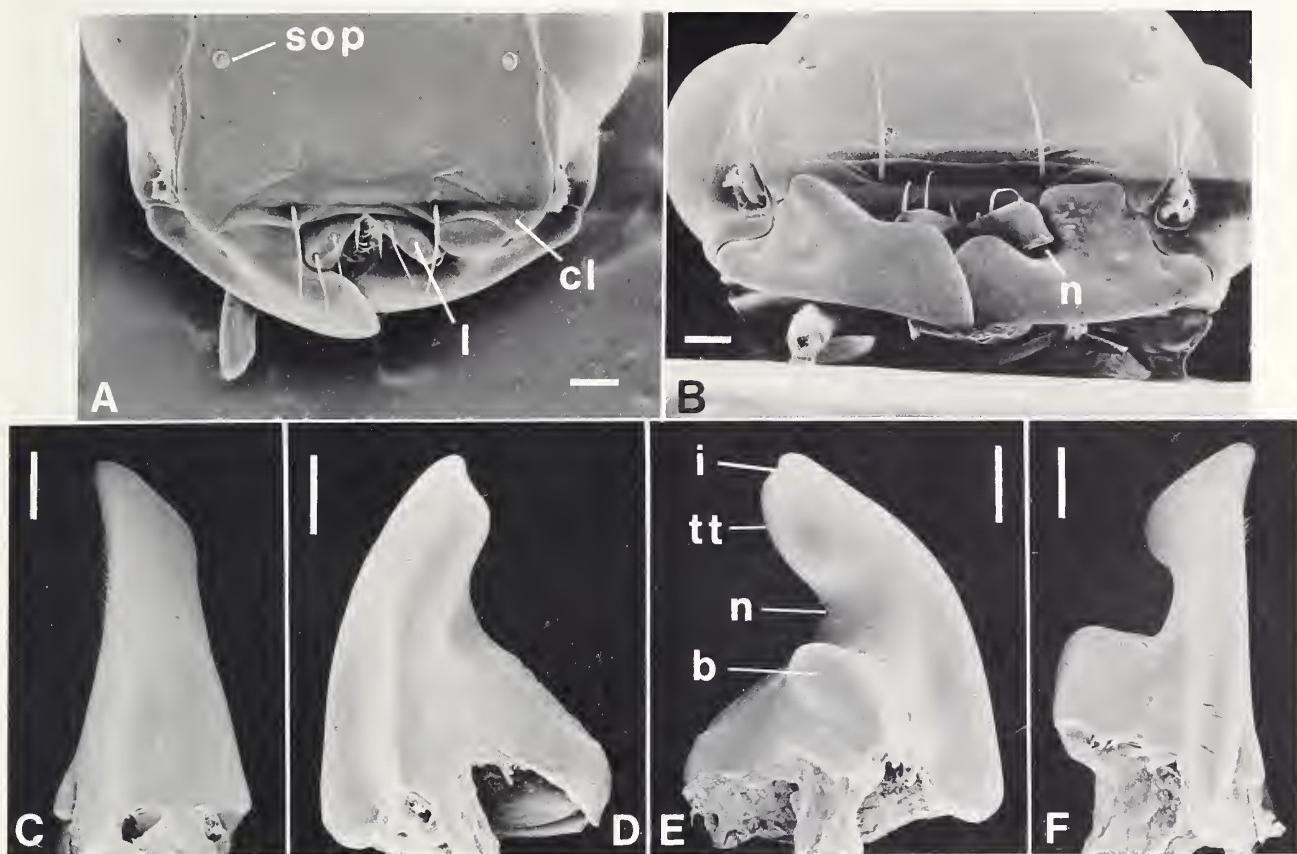


Fig. 20A–F. SEM photographs of anterior part of head and mandibles of *Badister grandiceps* Casey and *B. reflexus* LeConte. A–B, *B. grandiceps*: A, head, labrum and mandibles, dorsal aspect; B, same, frontal aspect. C–F, mandibles of *B. reflexus*: C–D, left mandible, lateral and dorsal aspects, respectively; and E–F, right mandible—dorsal and lateral aspects, respectively. Legend: b, basal boss; cl, clypeus; i, incisor; l, labrum; n, notch; sop, supraorbital setigerous puncture; tt, terebral tooth. Scale bars = 100  $\mu$ m.

represents an evolutionary reversal. In turn, this reversal is associated with life in an environment different from the environment occupied by most species of *Badister*.

**Microsculpture of the head in the *reflexus* group.**—Most species of *Badister* exhibit isodiametric sculpture on the dorsal surface of the head capsule. Adults of *B. ocularis* exhibit such sculpture (Fig. 21E–F; the left supraorbital setigerous puncture [sop] is shown, for orientation). A related species, *B. grandiceps* Casey, exhibits sculpture on the vertex that is slightly transverse (Fig. 21G–H). Although the difference is not much, and is not easily perceived even with relatively high power of a dissecting microscope, it is sufficient to cause structural color, so that the vertex of a typical *B. grandiceps* adult has a rather indistinct band of purple coloring on the vertex.

#### Geographical distribution of *Badister*

Ball (1959:190) reported *Badister* to be represented on every continent except South America. Recently, I saw a specimen with the character states of *Baudia* from Tucuman, Argentina, collected in January, 1979 by R. Goldbach (CNCI). Also, I participated in collecting a series of specimens with the characteristics of subgenus *Badister* in Amazonian Peru. These species will be studied and described, not necessarily by me, at some future date.

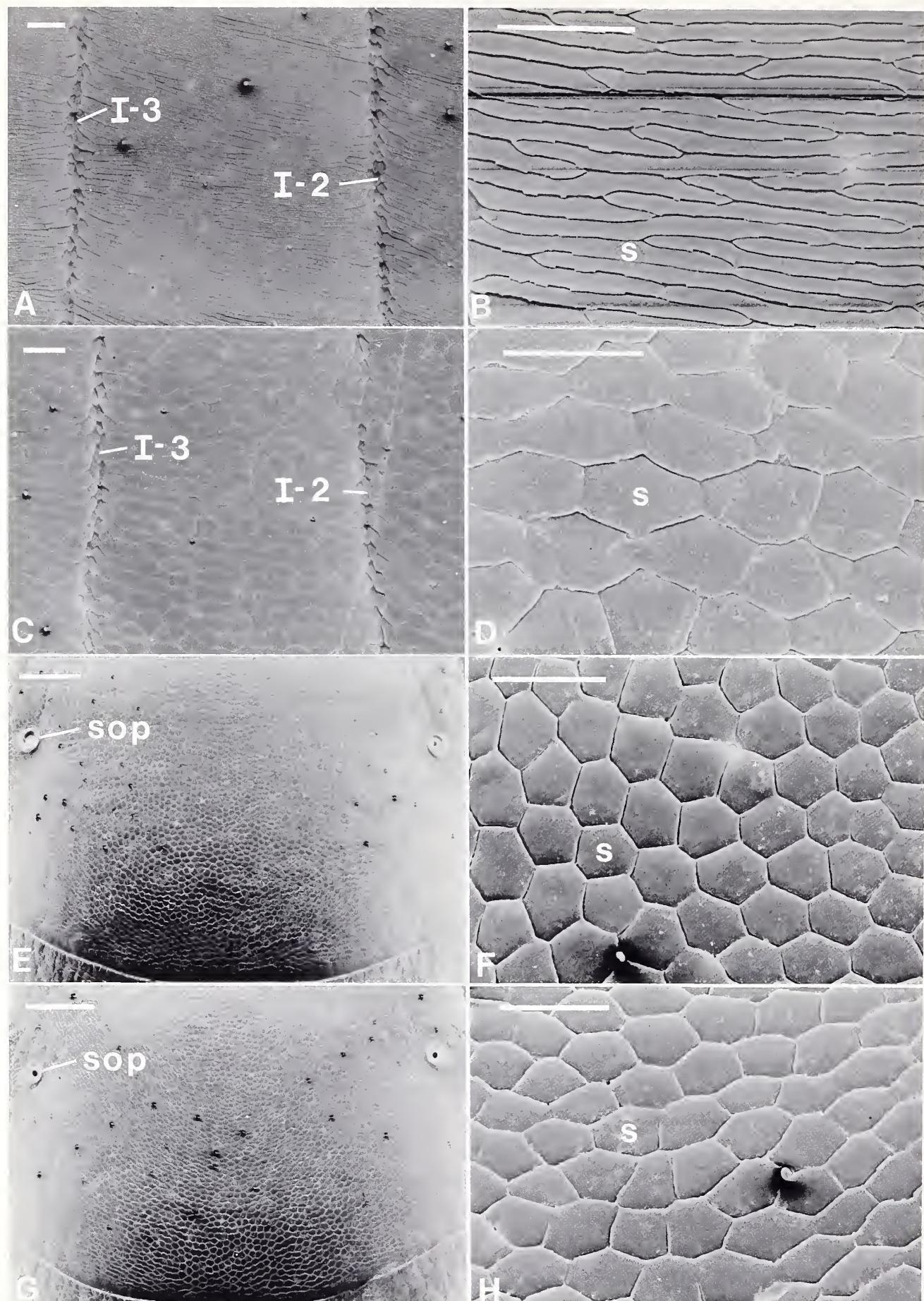


Fig. 21A–H. SEM photographs of microsculpture on various sclerites of members of *Badister* Clairville: A–B, interval 3, left elytron, of *B. neopulchellus* Lindroth; C–D, same of *B. obtusus* LeConte; E–F, vertex of head of *B. ocularis* Casey; G–H, same of *B. grandiceps* Casey. Legend: I-2, interneur 2; I-3, interneur 3; s, sculpticell; sop, supraorbital setigerous puncture. Scale bars: A–D, F, H = 20  $\mu\text{m}$ ; E, G = 100  $\mu\text{m}$ .

### Notes and new distribution records

Provided here for selected species are observations about variation, and about geographical distribution, including range extensions. The species sequence is the same as in Ball (1959:189–228).

#### *Badister neopulchellus* Lindroth

This is a wide-ranging species in North America, from the boreal forest in the north southward to Georgia in the east, and Texas, in the west. A record not previously published, extending the range of *B. neopulchellus* southward in the west, is based on a single female: U.S.A. CALIFORNIA San Bernardino County. Mountain Pass, IV.11.1942; O. Bryant (CASC).

#### *Badister obtusus* LeConte

Basically northern and wide-ranging in the boreal forest, *B. obtusus* is distributed southward only at higher altitudes in the Rocky Mountains and outlying ranges. New records are the following.

CANADA. NORTHWEST TERRITORIES. 2 females, Fort Wrigley, IX.27.1929; O. Bryant (CASC).

U.S.A. NEW MEXICO. San Miguel County. Sangre de Cristo Mountains, 3.2 km W Gascon, Rio de Gascon, 2,438 m, VIII.8.1963; G. E. & K. E. Ball (UASM).

TEXAS. Culberson County. Male, Guadalupe Mts., Nat. Park, Bocil, 2,407 m, IX.13.1988; R. S. Anderson (UASM).

#### *Badister elegans* LeConte

This species was known previously from the Great Plains states, southward to Brownsville, Texas. The following records establish its presence in northern México.

COAHUILA. Female, 31.2 km E San Pedro, V.31.1981; J. Doyen (UCBC).

TAMAULIPAS. Male, 3 females, 15.9 km W La Pesca, at U-V light, X.28.1965; G. E. Ball & D. R. Whitehead (UASM).

#### *Badister vandykei* Ball

The description of this species was based on a single male, collected in Baja California. The following record establishes occurrence of this species on the adjacent mainland of México.

SINALOA. Male, female, 41.8 km N Perico, VIII.13.1960; P. H. Arnaud, E. S. Ross & D. C. Rentz (CASC).

#### *Badister flavipes mexicanus* Van Dyke

The description of this subspecies was based on a single female collected at Oaxaca City, in southern México. Because the other subspecies were northern (Ball, 1959: 211–213), ranging as far south as Texas on the mainland and the Bahamas in the West Indies (Darlington, 1953), it was not unexpected that *B. f. mexicanus* would occur in much of the intervening area, and thus would be wide-ranging in México.

The following records confirm this expectation. Mainly eastern in distribution, the altitudinal range of *B. f. mexicanus* extends from near sea level to about 1,500 m. Specimens were collected in sites ranging from mesic to wet (i.e., palm savanna). During daylight hours, specimens were found under cover (principally leaf litter). Some were collected at U-V light at night, indicating nocturnal flight activity.

CHIAPAS. 4 females, Aguatenango, pasture-lake (under cow droppings, near water), VI.26.1972; G. E. Ball & P. E. Meyer (UASM). Male, Palenque ruins, U-V light, 91.4 m., V.22.1972; G. E. Ball, K E. Ball & P. E. Meyer (UASM).

MORELOS. 4 females, Santa Rosa, 5.1 km N Zacapec, 975 m, II.31.1966; M. W. McFadden & D. R. Whitehead (UASM). 4 males, female, 8.7 km E Cuernavaca, pedregal, 1,420 m, U-V light, V.29–30.1966; Ball & Whitehead (UASM), Male, Tejalpa, VI.23.1963; Whitehead (UASM).

NUEVO LEON. Female, Santa Rosa Canyon, 23.8 km W Linares, 732 m, U-V light, VII.6–7.1966; Ball & Whitehead (UASM).

OAXACA. Female, Oaxaca (city), XI.1968; G. Pollard (UASM). Female, Pueblo Nuevo, VIII.1–12.1986; H. & A. Howden (UASM).

SAN LUIS POTOSI. 2 females, El Salto Falls, U-V light, VII.7.1966; R. E. Woodruff (FSCA).

PUEBLA. Male, Puente Ahuehueyo, ca. 10 km W jct. Hwys 115 & 190, 1,280 m, VIII.10.1965; Ball & Whitehead (UASM).

TABASCO. Male, female, S. Ciudad Pemex, 53 m, U-V light, V.22.1972; Ball, Ball & Meyer (UASM).

TAMAULIPAS. Male, 2 females, Sierra de Tamaulipas, Hwy. 180, 76.6 km N Aldama, ca. 150 m, palm savanna, XII.8.1978; Ball & Ball (UASM). 2 males, Gomez Farias, Nacimiento del Rio Frio, VI.29.1969; S. & J. Peck (UASM).

#### *Badister reflexus* LeConte

Geographical variation.—As noted above, either the left or right mandible of adults of this species is notched. On the mainland (Yucatan Peninsula to southern Ontario) and in the Bahamas archipelago in the West Indies, only the left mandible is notched. In the Greater Antilles and Cayman Islands, either the left or right mandible is notched, as indicated in Table 8. A notched right mandible is predominant in Hispaniola and the Cayman Islands, while a notched left mandible is predominant in Cuba and Jamaica. However, the sample sizes are too small to be confident that the suggested pattern reflects reality.

Geographical distribution and localities.—This species was known to be wide-ranging in eastern United States and adjacent parts of southern Canada, from Ontario to "Texas" (no specific locality), and eastward to the Bahamas and Greater Antilles. The following list documents occurrence of *B. reflexus* in Texas, the West Indies and México.

U.S.A. TEXAS. Cameron County. Female, Brownsville, X.42; E. S. Ross (CASC).

MEXICO. QUINTANA ROO. 4 males, 5 females, 5 km W Chetumal, Hwy. 186, mercury vapor & U-V light, V.20.1987; E. G & T. J. Riley (LSUC).

WEST INDIES. BAHAMAS. 2 males, Rum Cay, nr. Port Nelson, III.16.1953; Van Voast (AMNH). Male, female, Cat Island, Arthur's Town, VII.29.1935; W. J. Clench (MCZC).

CAYMAN ISLANDS. 5 males, 5 females, Grand Cayman, South Sound, light trap B, IV.17–VIII.26.1938; C. B. Lewis & G. H. Thompson (MCZC).

CUBA. Female, Baragua, XI.12.1925; G. F. Stahl (MCZC). 2 males, 2 females, Cienfuegos, Soledad, IV–X.1926, 1936; P. J. Darlington, Jr. (MCZC). Female, Imias Camaguey, 8-1966, F. de Zayas (MCZC).

HISPANIOLA. Dominican Republic. 3 males, 2 females, Sanchez, VIII.1938; P. J. Darlington, Jr. (MCZC). Male, 2 females, Puerto Plata, VIII.29–IX.2.1938; P. J. Darlington, Jr. (MCZC). HAITI. 3 females, swamps N. Dessalines, IX.11.1934; P. J. Darlington, Jr. (MCZC).

JAMAICA. Male, Clarendon Parish, Portland Ridge, nr. Jackson Bay Cave, 12 m, V.4.1973; D. & M. Davis (USNM). Female, Good Hope, VIII.11.1966; H. F. Howden (CNCI).

#### *Badister parviceps* Ball

The original description of this species (Ball, 1959:225–226) was based on material from the central and northeastern states, and from eastern Ontario. Lindroth (1969: 967) reported additional localities in Manitoba and eastern British Columbia, and suggested that *B. parviceps* probably is transcontinental in distribution. This species is less hygrophilous than the other members of the *reflexus* group, occurring in leaf litter in mesic, shaded sites that are not in direct contact with standing water. Below are noted localities from farther south, extending the known range of this species to eastern Texas.

U.S.A. TEXAS. Brazos County. Female, Koppe's Bridge, ca. 8 km SW college Station, berlese, III.10.1988; R. S. Anderson (UASM). Male, same as above, but with note: riparian ravine, leaf litter, berlese (UASM). Houston County. Male, female, Big Slough Wild Area, FR 517 & Four C's hiking trail, bottomland, hardwood, litter, berlese, V.9.1988; Anderson (UASM). Tyler County. Male, female, 4.5 km W, 3 km N, Spurger Beech Wood Trail, litter, berlese, IV.24.1988; Anderson (UASM). Walker County. Female, Huntsville State Park, pine-hardwood forest, litter, berlese, IV.14.1988; Anderson (UASM).

#### *Badister submarinus* Motschulsky

I doubted that this species, known only from two females ostensibly collected at Sacramento, California, was a North American resident, imagining instead that the specimens had been collected elsewhere and had been mislabelled. Lacking a male for study, I included this species in subgenus *Baudia*, *incertae sedis*, because the classification of the species of this group is based on male characters (Ball, 1959: 228). About eight years ago, I found in material for identification sent from the Zoological Museum at Copenhagen (ZMUC), a third specimen (also a female) of *B. submarinus*, labelled: "Oregon, U.S.A."; "Upper Klamath Lake at Algoma, Klamath Co. Oregon"; "4100 ft. 11.X.1949 E. Suenson." This record confirms that *B. submarinus* is a western North American resident. However, it must remain *incertae sedis* until a male is located and its genitalia studied.

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I am grateful to J. K. Liebherr for undertaking to organize the *Festschrift* in honor of J. G. Franclemont, and for inviting me to prepare a contribution to it.

A major part of this paper is the set of plates of photographs taken with the Scanning Electron Microscope. They, and the structures illustrated, were prepared in a cooperative operation by G. D. Braybrook, D. Shpeley, and J. S. Scott, who are technologists in my Department. Mr. Scott prepared also the habitus photograph of *Dicaelus franclemonti*, and final versions of the maps and other figures.

G. Scherer, of the Zoologische Staatssammlung, München, made me welcome during a visit to his institution, and arranged for the loan of the type series of *Pterostichus karikali*. Y. Bousquet, of what is now the Division of Biological Resources, and was formerly the Biosystematics Research Centre, Ottawa, made it possible for me to examine the licinines in his care during several visits to his institution. N. E. Stork, of The Natural History Museum, London, responded with alacrity to my frantic request for last-minute assistance. David H. Kavanaugh, of the California Academy of Sciences, San Francisco, arranged for the loan of an extensive array of licinines that I had not seen previously. I appreciate very much the special assistance of these colleagues, and as well, the cooperation of the other curators and collections managers whose names appear in the list of institutions from the collections of which study material was received.

As I learned so well from my association with Jack Franclemont, much of the pleasure of systematic entomology is obtained through life in the field, where one hunts out and assembles the specimens and knowledge that make possible all of the subsequent descriptions and analyses. The pleasure that I enjoyed in finding the *Liodicaelus* material in the mountains of northern México and southwestern United States was enhanced by association with the late D. R. Whitehead, and D. Shpeley, H. E. Frania, S. McCleve and W. Fraga. Not only did I enjoy their company, but I appreciated as well the specimens that they found. My wife's name appears on many of the specimen labels, and I am pleased to acknowledge her contributions, also.

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**TAXONOMY AND DISTRIBUTION OF  
THE ATHETINE GENUS *LYPOGLOSSA* FENYES  
(COLEOPTERA: STAPHYLINIDAE: ALEOCHARINAE) IN  
NORTH AMERICA, WITH DESCRIPTION OF A  
NEW SPECIES**

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*Abstract.*—The athetine genus *Lypoglossa* Fenyes is reviewed and redescribed. Two North American species are treated, of which one is described as new: *franclemonti* from the boreal region of northern North America. The following new specific synonymy is proposed: *fenyesi* Bernhauer 1907 (=*angularis* Mäklin, 1853). Lectotypes are designated for *Lypoglossa fenyesi* (Bernhauer) and the Palearctic species *L. lateralis* (Mannerheim).

Adult mouthpart structures are illustrated for the first time for the genus; species distributional data are recorded and mapped; all bionomic data are presented; habitus, male aedeagus, female spermatheca, and other diagnostic characters are illustrated with the aid of line drawings and scanning electron photomicrographs; and a key to species is provided.

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The genus *Lypoglossa* was proposed by Fenyes in 1918 to contain the single species *Dasyglossa fenyesi* Bernhauer (1907:402) described from the Pacific Northwest. During the next half century, no important contributions were provided on the systematics of this little known genus of athetine Aleocharinae. In 1978, C. H. Seevers, in his tribal and generic revision of North American aleocharine rove beetles, gave little information on this taxon and its characters, other than to include it in a key to genera (p. 46). Our knowledge of the genus was further amplified in 1985, when Lohse and Smetana, while studying numerous types of species of oxypodine and athetine staphylinids described by Mannerheim and Mäklin from northwestern North America, noted that *Myrmecodia angularis* Mäklin (1853:181) belonged to the genus *Lypoglossa*; in their paper they formalized this new combination, thus adding a second species of this genus to our faunal list. In their discussion, Lohse and Smetana gave a brief diagnosis to differentiate *L. angularis* and *L. fenyesi*, based on characters of the antenna, color and shape of the pronotum, and male and female genitalia. They also synonymized the Palearctic genus *Megacrotona* Scheerpeltz (1968:159), including the single species *M. lateralis* (Mannerheim), with *Lypoglossa*.

The present paper resulted in part from my request to examine unidentified specimens of Staphylinidae in the collection of the University of Vermont, in particular the aleocharine rove beetles. To my surprise, included in this material were specimens of a large, distinctive athetine from the high elevations of southern Vermont which at first I was unable to name but later tentatively identified as belonging to the genus *Lypoglossa*. Other borrowed material, from collections listed in Acknowledgments, included specimens from high elevations of northern New York and New Hampshire, a bog in Maine in the East, and numerous localities in western North America. In

this paper, I provide a detailed redescription and diagnosis of the genus *Lypoglossa* with illustrations of adult habitus, mouthparts, and other structural characters, new synonymy, lectotype designations, description of a new species, and a key to aid in the identification of the North American species.

### Genus *Lypoglossa* Fenyes

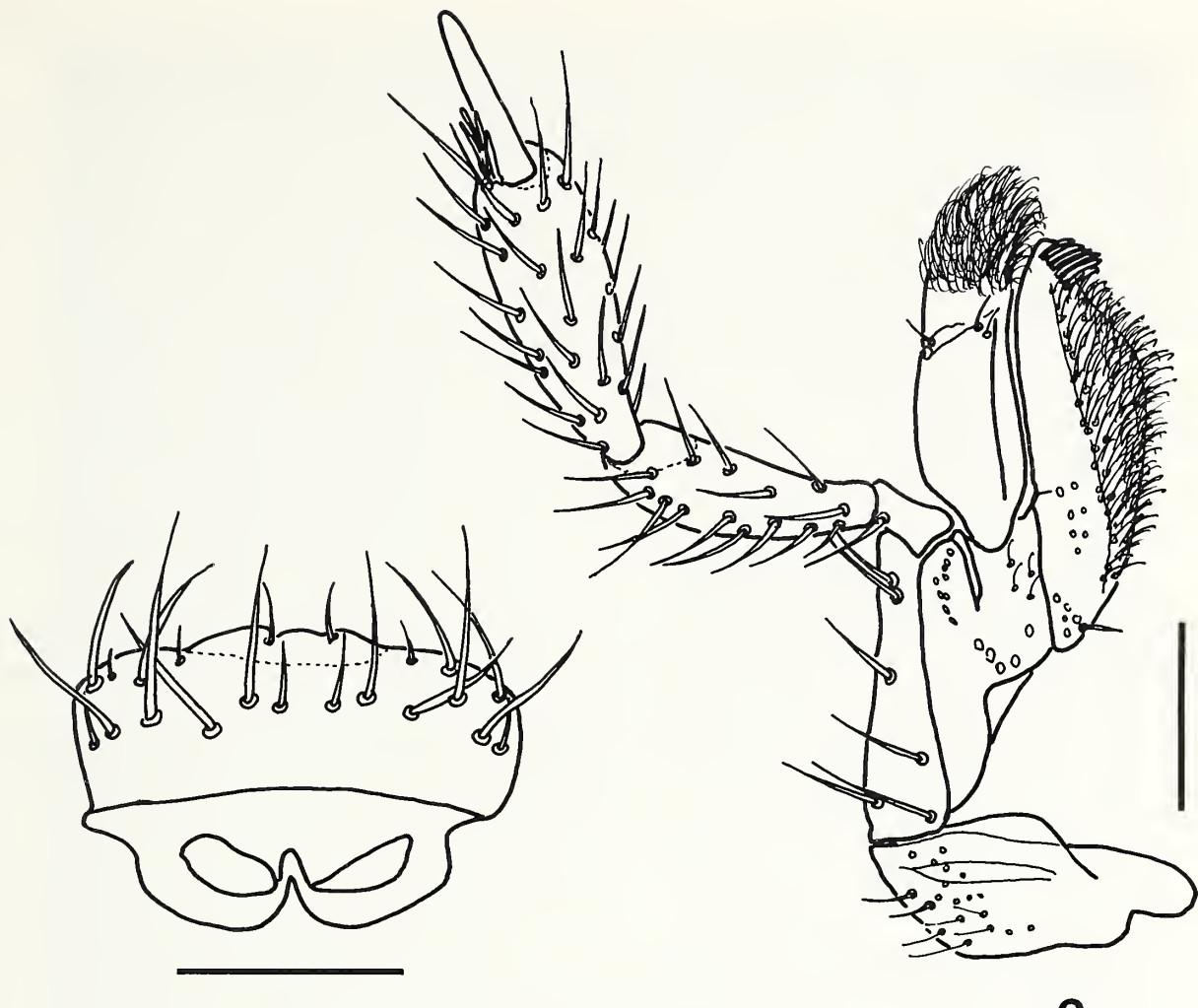
*Lypoglossa* Fenyes, 1918:23; 1920:239; Blackwelder, 1952:228; Moore and Legner, 1975:448; Seevers, 1978:46, 134. Type species: *Dasyglossa fenyesi* Bernhauer, 1907: 402, by monotypy.

*Megacrotona* Scheerpeltz, 1968:159 (as new subgenus of *Atheta*); Lohse and Smetana, 1985:294 (as junior synonym of *Lypoglossa*). Type species: *Oxypoda lateralis* Mannerheim, 1830:484, by monotypy.

**Diagnosis.** Members of *Lypoglossa* share a striking overall resemblance to *Devia prospera* Erichson (Oxypodini), and to some large specimens of *Oxypoda* (Oxypodini), but differ principally by the 4,5,5 tarsal formula (5,5,5 in *Devia prospera* and *Oxypoda* spp.) and the unique punctuation and pubescence of the dorsal abdominal segments (Fig. 5) in which terga III-V are densely, finely punctured, with short, silky, dense, appressed microsetae, whereas terga VI–VIII are very sparsely punctured, with sparse microsetae (uniform punctuation and microsetae on dorsal abdominal segments in *Devia prospera* and *Oxypoda* spp.). *Lypoglossa* can be further characterized by the following combination of characters: relatively large (3.3–4.5 mm), fusiform in shape; pronotum exceptionally broad, 0.69–0.79 × wider than long; pronotal pubescence along midline directed cephalad, remaining microsetae swirling laterad from midline (Pattern E of Seevers, 1978) (Fig. 5); hypomera incompletely visible from lateral view; mesocoxae narrowly separated; mesosternal process long, slender, acute at apex (Fig. 8); mesosternal process: isthmus: metasternal process ratio, 12:5:1; tarsal formula 4,5,5.

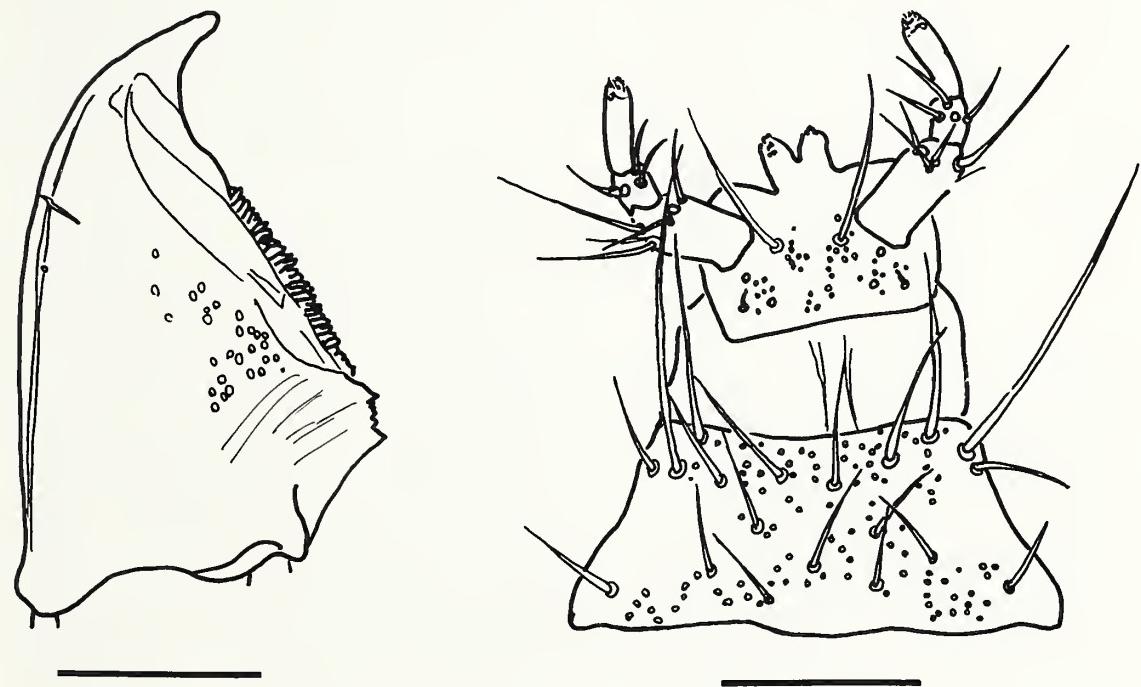
**Redescription.** Moderate to large sized, length of North American specimens 3.3–4.5 mm. Body shape elongate, fusiform (Fig. 5). Body color testaceous to reddish-brown, except head and abdomen dark reddish-brown to piceous. Body microsculpture imbricate, dense and prominent on head, pronotum, and elytra (Fig. 9); that on abdominal segments transversely striate, consisting of obsolete, interconnected, wavy microlines; cuticular surface dull to slightly glossy; integument moderately to densely pubescent, microsetae appressed; macrosetae present, conspicuous on abdomen; punctures moderately dense throughout, very fine to slightly asperate, especially on basal three abdominal segments.

Head more or less transverse, slightly wider than long (L/W ratio = 0.84), broadest across temples just posterior to eyes, basal angles broadly rounded, neck absent. Eye size small, 0.40 × length of head. Tempora moderate, subequal to length of eye, broadly rounded. Dorsal pubescence prominent, directed more or less medially on sides, and anteriorly along midline. Infraorbital ridge conspicuous posteriorly, absent anteriorly. Antenna moderately elongate, about as long as, or slightly longer than head and pronotum combined, slightly incrassate towards apex; articles 1–4 more or less elongate, article 3 longer than 2, articles 5–10 becoming more gradually transverse and increasing in width to apical articles; article 11 conical apically, about as long as articles 9 + 10.



1

2



3

4

Figs. 1–4. *Lypoglossa franclemonti*, adult mouthpart structures. 1, Labrum, dorsal aspect; 2, Maxilla, dorsal aspect; 3, Left mandible, dorsal aspect; 4, Labium, ventral aspect. (Scale line = 1.0 mm)

Labrum transverse (Fig. 1). Right and left mandibles with similar dentition (Fig. 3), without internal teeth, apices acute, entire; molar region slightly developed, with short row of spinose teeth on inner edge; membranous prostheca finely serrated medially. Maxilla (Fig. 2) with galea slightly longer than lacinia; galea densely pubescent in apical 0.4; lacinia with comb of single row of 6–7 large recurved teeth apically, and dense patch of recurved setae dorso-medially; maxillary palps 4-segmented. Labium as in Figure 4; ligula moderately short, deeply cleft nearly to base into 2 bluntly rounded, divergent lobes; 2 medial setae, broadly separated at base; prementum with numerous pseudopores medially plus posterior to medial setae, several pseudopores, 2 large real pores, and 1 spinose pore laterally on each side; labial palps 3-segmented, chaetotaxy of articles as in Figure 4; mentum and chaetotaxy as in Figure 4.

Pronotum broadly transverse, about  $0.69-0.79 \times$  wider than long; anterolateral margins obtusely rounded; sides broadly, evenly arcuate; posterior margin ranging from broadly arcuate to distinctly bisinuate; pubescence with microsetae directed cephalad in a narrow median strip, with remaining microsetae directed laterad from median row in swirling pattern as in Figure 5 (Pattern E, *sensu* Seevers, 1978, or Type I, *sensu* Hoeg, 1945).

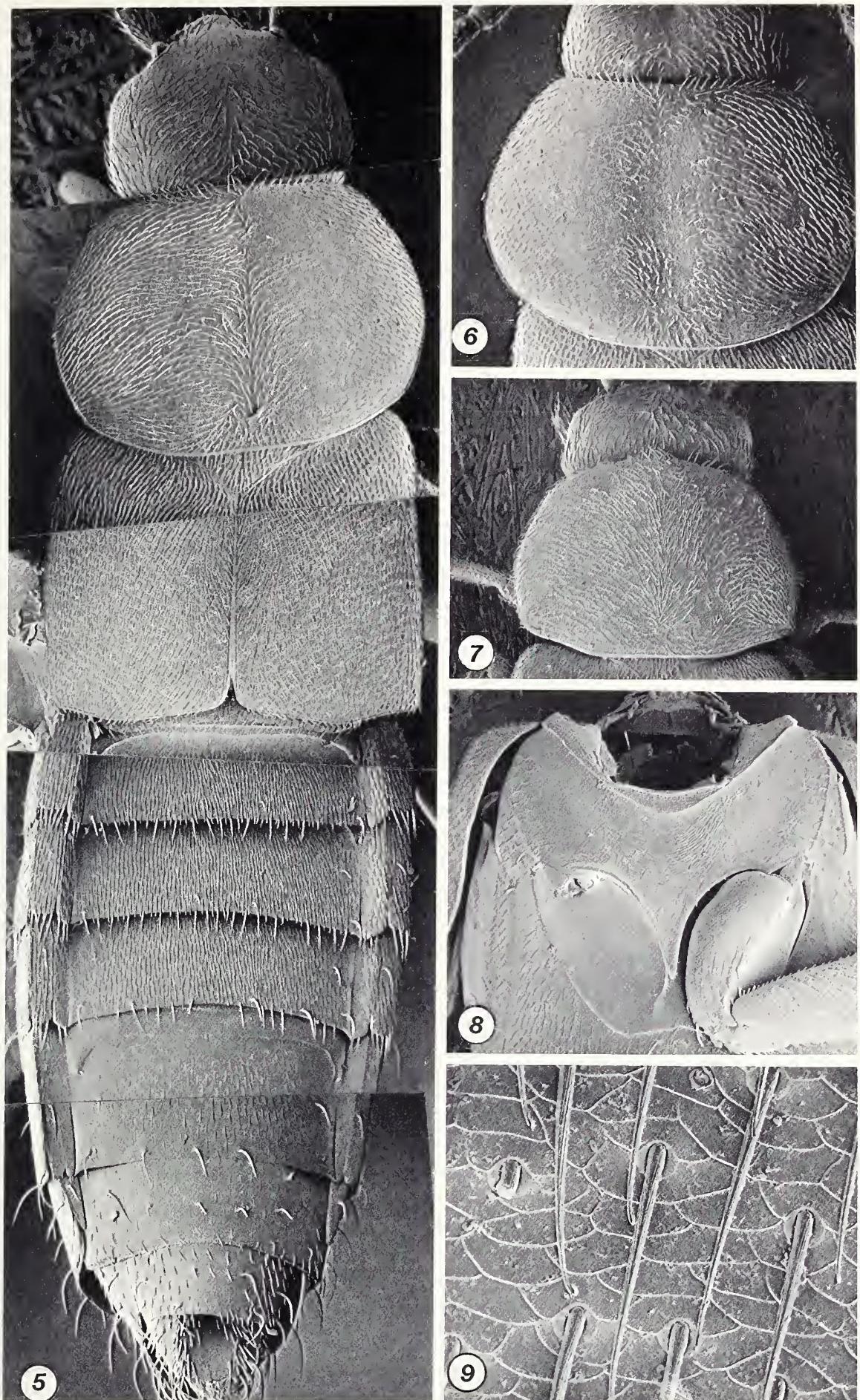
Elytra relatively short, slightly longer than pronotum, parallel-sided; outer apical angles strongly sinuate; pubescence dense, microsetae arranged in slightly sinuate pattern, directed more or less posteriorly, as in Figure 5. Mesosternum with narrow mesosternal process (Fig. 8), elongate, apically pointed, extending to slightly beyond middle of coxal cavities; metasternal process short, broadly rounded; isthmus relatively long; coxae narrowly separated, acetabulae finely margined posteriorly. Mesosternal process: isthmus: metasternal process ratio 12:5:1. Legs slender, long; tarsal formula 4,5,5; hind tarsus elongate, tarsomeres 1–4 decreasing in length.

Abdomen broad at base, elongate, tapered from basal segments to apex. Terga III–VI slightly, transversely impressed basally; basal impressions impunctate, smooth. Terga III–V dull, densely punctured, with short, silky, appressed microsetae. Terga VI–VIII less dull, very sparsely punctured and pubescent.

*Secondary sexual characteristics. Male:* Dorsum of head, and broad to narrow median area of pronotum moderately impressed (as in Fig. 6). *Female:* Dorsum of head evenly convex; pronotum evenly convex with slight narrow impression along median line in some specimens (as in Fig. 5). [The head and pronota of specimens of the type series of the Palearctic species *L. lateralis* (Mannerheim), including both sexes, are evenly convex dorsally without any apparent median impression.]

*Distribution.* At the present time, the known Nearctic species have a transcontinental, northern distribution, with relict populations in the mountains or high elevations of more southern areas. The only known Palearctic species is also widely distributed in the high elevations of northern and middle Europe, and Siberia (Scheerpeltz, 1968; Benick and Lohse, 1974).

*Bionomics.* Limited distributional and ecological evidence would suggest that members of *Lypoglossa* are probably restricted to the boreal forest zone of North America (and Eurasia), a coniferous forest with a floor cover of mosses or of low herbs and shrubs, interspersed with extensive lakes (Rowe, 1972), which extends in a continuous belt from Newfoundland and the Labrador coast in the east, west to the Rocky Mountains and then northwards to the mouth of the Mackenzie River



Figs. 5–9. *Lypoglossa* spp.: 5–6 & 8–9, *L. franclemonti*. 5, Dorsal habitus; 6, Pronotum, dorsal aspect, male; 8, Meso- and metasternum; 9, Elytral microsculpture. 7, *L. angularis*, Pronotum, dorsal aspect, female.

and the central areas of Alaska (with relictual areas in the mountains of Arizona, New Mexico, and Colorado, and high elevations of eastern New York through New England) (Scudder, 1979). The principal tree species of the boreal forest include White and Black Spruce, various pine and fir species, and White Birch, Trembling Aspen and Balsam Poplar (Scudder, 1979).

*Remarks.* *Lypoglossa*, as now known, consists of 2 widely distributed boreal species in North America and 1 species in the Palearctic region.

Having amassed a considerable number of specimens of both identified and unidentified North American material from various collections, I assumed these specimens, segregated into 2 distinct, but similar morphospecies, would be readily assignable to the two available North American names. However, this was not the case. After careful examination of the types of *Lypoglossa angularis* (Mäklin) and *L. senyesi* (Bernhauer), I discovered that they are conspecific, thus necessitating the new synonymy stated herein, and the description of a new species.

Most specimens of *Lypoglossa* in collections, if determined, are identified as *L. senyesi*, thought originally to be the only included species of the genus. The new species, *franclemonti*, described herein, is often included in identified series of *L. senyesi*. Specimens of both species, however, can be separated readily by the shape of the pronotum, and by key differences in the male genitalia.

#### KEY TO NORTH AMERICAN LYPOGLOSSA

1. Pronotum less transverse, broadly oval in shape ( $L/W$  ratio = 0.75–0.79), posterior margin usually evenly arcuate, with posterior angles broadly rounded (as in Figs. 5–6), pronotal color testaceous to light reddish-brown, usually strongly contrasting with darker color of head and elytra; median lobe of aedeagus and apical lobe of paramerite as in Figs. 10–12 ..... *L. franclemonti*, n. sp.
- 1'. Pronotum more transverse, rectangular in shape ( $L/W$  ratio = 0.69–0.71), posterior margin usually distinctly bisinuate, with posterior angles strongly obtuse (as in Fig. 7), pronotal color dark reddish-brown, usually concolorous with elytra, or only slightly contrasting; median lobe of aedeagus and apical lobe of paramerite as in Figs. 15–17 ..... *L. angularis* (Mäklin)

#### *Lypoglossa franclemonti*, new species

Figs. 1–6, 8–14; Map 1

*Lypoglossa senyesi*: *sensu* Lohse and Smetana, 1985:294 (not Bernhauer).

*Diagnosis.* *Lypoglossa franclemonti* is very similar externally to *L. angularis*, but can be readily separated by the more oval, less transversely-shaped pronotum with broadly arcuate posterior margin and evenly rounded posterior angles (Figs. 5–6), by the reddish-yellow pronotum which is usually contrasting with the head and elytra, and by the characteristic shape of the median lobe of the aedeagus (Figs. 10–11) and the apical lobe of the paramerite (Fig. 12).

*Description.* Length 3.3–4.5 mm. Body color testaceous to yellowish brown, except head, areas of elytra adjacent to scutellum and elytral suture, sometimes outer posterior angles of elytra, and abdominal segments darker, reddish-brown to piceous; in most specimens terga VI–VIII with bluish-black iridescent sheen.

Head obsoletely imbricate with moderately dense, irregular, wide, transverse sculp-

ticells, surface slightly glossy; microsetae moderately short, somewhat dense, appressed; punctures fine to very slightly asperate. Antenna elongate and slender, with articles 1–3 elongate, article 1 slightly incrassate, article 2 more slender, slightly shorter than article 3; article 4 distinctly longer than wide; articles 5–10 decreasing in length and becoming more quadrate and transverse; article 11 subequal to articles 9 + 10.

Pronotum less transverse, tending to be somewhat oval-quadratae (L/W ratio = 0.75–0.79); posterior margin broadly arcuate, or very obsoletely bisinuate in some specimens; posterior angles broadly rounded. Integument markedly imbricate, moderately glossy; pubescence with microsetae moderately short, dense, appressed, directed cephalad in narrow median strip, with remaining microsetae swirling laterad from median strip; punctures moderately fine, very slightly asperate.

Elytra slightly narrower than maximum width of pronotum; microsculpture densely imbricate (Fig. 9); pubescence with microsetae short, dense, appressed, directed posteriorly in a slightly sinuate pattern; punctures dense, uniform, slightly asperate.

Abdominal terga III–V with moderately dense pubescence; microsetae very fine, short, appressed; punctures fine, dense. Tergite VI with sparse, fine punctures; terga VII–VIII with punctures even more sparse than that of tergite VI; microsetae of terga VI–VIII moderately short, silky, fine, appressed; abdominal integument dull, with fine, transverse microsculpture, appearing (in most specimens) iridescent (especially terga VI–VII).

Male: Median lobe of aedeagus as in Figures 10–11. Paramere and apical lobe of paramerite as in Figure 12.

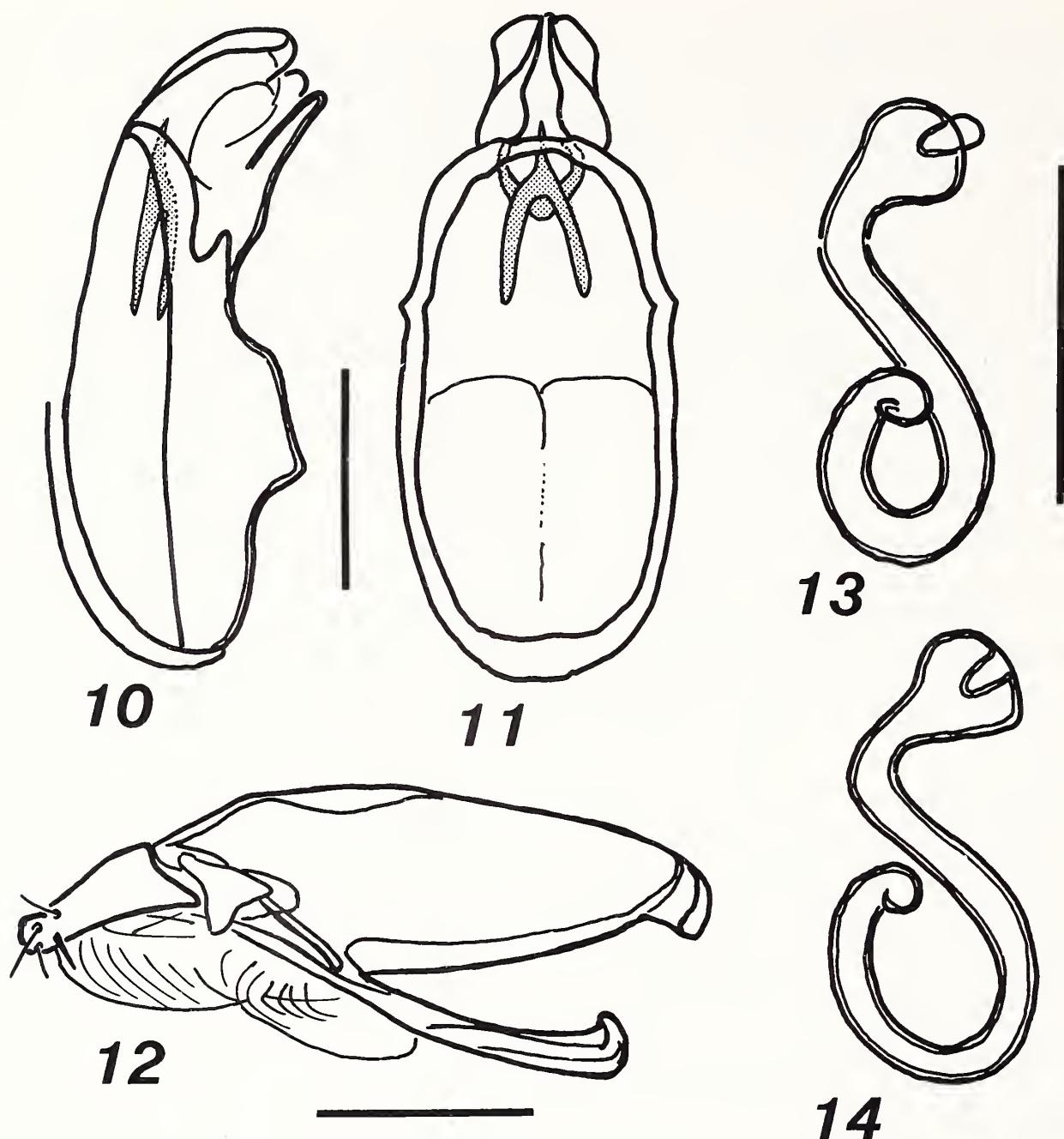
Female: Spermatheca as in Figures 13–14.

*Secondary sexual characteristics.* *Male:* Dorsum of head, and broad area along median line of pronotum impressed (Fig. 6). *Female:* Dorsum of head and pronotum evenly convex (in most specimens pronotum may be narrowly impressed along median line) (Fig. 5).

*Types.* Holotype, male, with labels: Mt. Whiteface, N.Y. [Essex Co.], 2,000–4,000 ft, 22 Aug. 1916/HOLOTYPE *Lypoglossa franclemonti* ♂, design. 1991, E. R. Hoebeke/HOLOTYPE Cornell U. No. 6510. Allotype, female, with labels: Artist's Brook, Essex Co., N.Y., June 11, 1933, H. Dietrich/ALLOTYPE *Lypoglossa franclemonti* ♀, design. 1991, E. R. Hoebeke/ALLOTYPE Cornell U. No. 6510. Both holotype and allotype are deposited in the Cornell University Insect Collection, Ithaca, N.Y.

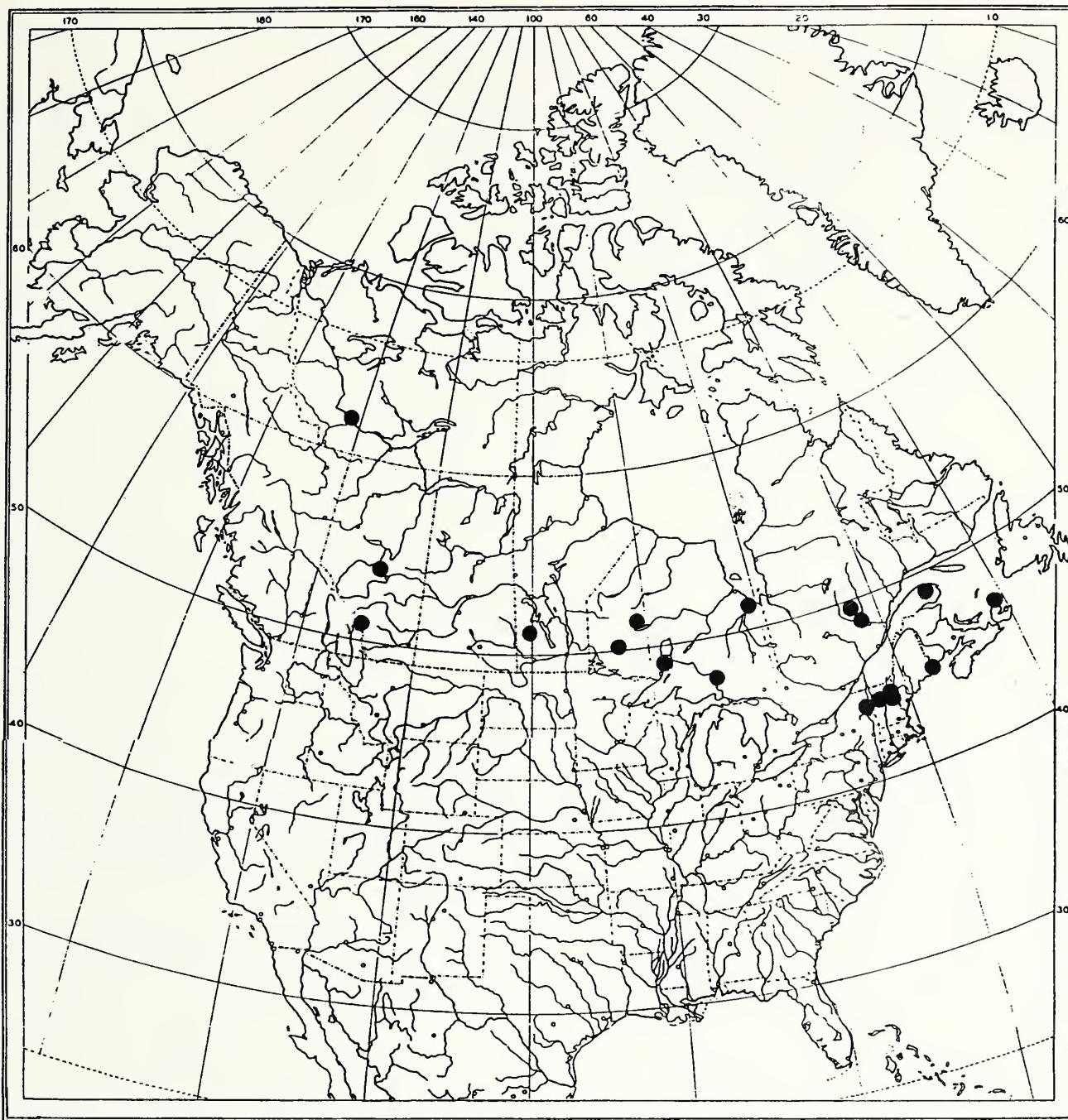
Paratypes, 182, are deposited in the CNCI, MCZC, FMNH, CUIC, SEMC, UVCC, and DENH.

*CANADA: Alberta:* 8 mi W Calgary, on 1A, 18–20-VI-1980 (CUIC, 2). George Lake, ca. 53°57'N, 114°06'W, 1–VI, 12–VI, 16–VI, 2–VIII, 10–VIII–1980, JS Ashe (SEMC, 16); George Lake, 53°57'N, 114°06'W, 1–X–1966, 10–IX–1966, 25–IX–1966, RE Leech (CNCI, 5). Lusk Creek, Kananaskis F.E.S., 14–VII–1971, JM & BA Campbell (CNCI, 4). *Manitoba:* Riding Mtn. N.P., Moon Lake, 17–IX–1979, A Smetana (CNCI, 6); nr Deep Lk., 7–IX–1979, A Smetana (CNCI, 4); Whirlpool Rv. at Hwy 19, 6–IX–1979, A Smetana (CNCI, 1). *Northwest Territories:* Hwy 3, 5 mi SE Ft. Simpson, 21–VI–1972, A Smetana (CNCI, 1). *Nova Scotia:* Cape Breton H.N.P., 410 m, Benjies Lake area, 18–IX–1984, JM Campbell & A Davies (CNCI, 1); 440 m, nr Sammy's Barren, 24.IX.1984, JM Campbell & A Davies (CNCI, 1). *Ontario:* Lk. Superior Prov. Pk., Garanya, 9–VI–1973, JM Campbell & R Parry (CNCI, 10);



Figs. 10–14. *Lypoglossa franclemonti*. 10, Median lobe of aedeagus, lateral aspect; 11, Median lobe of aedeagus, dorsal aspect; 12, Paramere; 13, Spermatheca (Bolton, Vermont); 14, Spermatheca (Mt. Marcy, New York). (Scale line = 0.25 mm)

Frater, 9–13-VI-1973, JM Campbell & R Parry (CNCI, 5); Old Woman Bay, 13-VI-1973, Campbell & Parry (CNCI, 3); Agawa Bay, 13-VI-1973, Campbell & Parry (CNCI, 6); Baldhead Lk., 8-VI-1973, JM Campbell & R Parry (CNCI, 1). 46 mi N Hurkett, Black Sturgeon Lk., 28–29-VI-1973, R Parry & JM Campbell (CNCI, 2). 49 mi N Savant Lake, 23-VI-1973, Campbell & Parry (CNCI, 1). Moosenoë, 30-VI-1973, 2-VII-1973, Parry & Campbell (CNCI, 7). 21 mi & 41 mi N Pickle Lake, 19-VI-1973, Campbell & Parry (CNCI, 2). 36 mi S Pickle Lake, 22-VI-1973, Campbell & Parry (CNCI, 5). Quebec: Mistassini Post, 13-VI-1956, JR Lansway (CNCI, 1). Parc des Laurentides, Mare-du-Sault, 2,700 ft, 15–17-VIII-1970, JM & BA Campbell (CNCI, 2). Gaspesie Parc, Lac St. Anne, 12-VII-1972, 1,500 ft, JM & BA Campbell (CNCI, 1); Lac du Diable, 12-VII-1972, 1,500 ft, JM & BA Campbell (CNCI, 2);



Map 1. Known geographic distribution of *Lypoglossa franclemonti*.

Lac Cascapedia, 14-VII-1972, 1,700 ft, JM & BA Campbell (CNCI, 1); Mont Albert, 9-VII-1972, 1,000 ft, JM & BA Campbell (CNCI, 4).

UNITED STATES: Maine: Washington Co., Carrying Place Cove, Lubec, 23-VII/24-VIII-1989, H. Främbis (CUIC, 22). New Hampshire: Coos Co., Crawford Notch, 25-IX-1908 (MCZC, 3); Bretton Woods (FMNH, 1); 1 mi NE East Inlet Dam, 27-IX/17-X-1986, 26-IX-1986, DS Chandler (DENH, 2); Norton Pool, 2 mi E East Inlet Dam, 7-IX-1984, DS Chandler (DENH, 2); White Mts., GlenBoulder Trail, 2,500 ft, 17-VIII-1976, JM & BA Campbell (CNCI, 1); Glen Ellis Falls, 1,900 ft, 15-VIII-1976, JM & BA Campbell (CNCI, 1). New York: Essex Co., Mt. Whiteface, 21-X-1934, CR Crosby (CUIC, 3); Mt. Whiteface, 25-VIII-1921 (CUIC, 1); Top Mt. Marcy, 22-X-1936, H Dietrich (CUIC, 1); Top of Mt. Whiteface, 22-X-1936, H Dietrich (CUIC, 2); Essex Co. (no locality), 10-VII-1918 (CUIC, 4); Top Mt. Mc-

Intyre, 1-VII-1923, CR Crosby (CUIC, 1); Artist's Brook, 11-VI-1933, H Dietrich (CUIC, 1). *Vermont*: Chittenden Co., Camel's Hump, Bolton, 3,800 ft, 7-VII-1972, RT Bell (UVCC, 11); same locality, 9-19-VIII-1972 (UVCC, 4); same locality, 1-VIII-1972, J Spence (UVCC, 6); same locality, VIII-IX-1972 (UVCC, 6); same locality, 24-VII-1972, 3790 ft (UVCC, 3); same locality, 18-VII-1973, 3,400 ft (UVCC, 2); same locality, 18-VII-1973, 3,800 ft (UVCC, 4); same locality, 17-VII-1972, 3,800 ft (UVCC, 6); same locality, 23-VIII-1975, Langworthy (UVCC, 1); Mt. Mansfield, 4,000 ft, 11-X-1969, HP Wimmer (UVCC, 1).

*Etymology.* This species is named in honor of Dr. John G. Franclemont, emeritus professor, Cornell University, who not only has made significant contributions to our knowledge of North American Lepidoptera, but also has been responsible for the training of many practicing North American insect systematists. In recognition of his eightieth birthday, it is with great pleasure that I name this new species after "Jack," my academic advisor as a graduate student, and now, a dear friend and colleague.

*Geographic distribution.* The known range of *L. franclemonti* includes localities in Alberta, Northwest Territories, Manitoba, western Ontario, Quebec, and Nova Scotia, with relict populations in the high elevations of eastern New York, Vermont, and New Hampshire, and a bog in Maine (Map 1).

*Bionomics.* Little is known about the habits of this species. It appears to prefer rather moist, rich, organic habitats. Most western specimens studied were taken from sifted litter in birch, birch-liedum, and black spruce bogs; from sifted leaf litter; and from sifted moss and lichens on rotten logs. A few additional eastern specimens bear the following habitat data: "pit traps" in spruce forest at 3,400–3,800 ft, "flight intercept trap," and "sift conifer logs." Most specimens examined were taken in June, July, and August, but also in September and October.

*Remarks.* Externally the types of *L. angularis* and *L. fenyesi* are identical, and detailed study of the genitalia of males from the syntype series of both supports the synonymy proposed below. The taxon "*L. fenyesi*" referred to in Lohse and Smetana (1985, under "Discussion," p. 294) is actually *L. franclemonti*. Apparently, Lohse and Smetana studied only the type of *L. angularis*; had they also examined the type series of *L. fenyesi* they would have discovered, as I did, that the types of both are conspecific and thus would have known that the other "widespread" species of *Lypoglossa* occurring in North America actually represented an undescribed species. The male and female genitalia figured in Lohse and Smetana (1985) as that of *L. fenyesi* (cf. Figs. 24–25, p. 295) is really that of *L. franclemonti*.

*Lypoglossa angularis* (Mäklin)

Figs. 7, 15–18; Map 2

*Myrmedonia angularis* Mäklin, 1853:181.

Lectotype male: UNITED STATES: Alaska: "Woskres." (=Woskersensk, Kenai peninsula) (UZMH). Specimen with labels: Coll. Mäklin; *Myrmedonia angularis* Mäkl. Woskres.; *Dasyglossa prospera* Er. det. Bernhauer; Mus. Zool. H. fors Spec. typ. No. 2270 *Myrmedonia angularis* Mäkl.; *Myremedonia angularis* Mäklin Lectotypus Lohse design. 1983. Type specimen studied. Genitalia dissected and mounted.

*Dasyglossa fenyesi* Bernhauer, 1907:402; Leng, 1920:126. New Synonymy.

Lectotype male: CANADA: British Columbia (FMNH). Specimen with labels: Em[era]ld Lake, BC, 0.6.6.26, DrAFenyes; 330.; *fenyesi* Brh. Typus.; Chicago NHMus, M. Bernhauer Collection; LECTOTYPE *Dasyglossa fenyesi* Bernhauer, design. 1991, E. R. Hoebeke. One paralectotype, male, with labels: Banff, Alta, 0.6.6.24, DrAFenyes; 313.; 103. (in red ink); *fenyesi* Brh. Cotypus.; Chicago NHMus, M. Bernhauer Collection; PARALECTOTYPE *Dasyglossa fenyesi* Bernhauer, design. 1991, E. R. Hoebeke (FMNH). Type material studied and lectotype here designated. Genitalia of lectotype dissected and mounted.

*Lypoglossa fenyesi*: Fenyes, 1920:239, t. 5, f. 2; Bernhauer and Scheerpeltz, 1926:

597; Hatch, 1957:145; Moore and Legner, 1975:448; Seavers, 1978:271.

*Lypoglossa angularis*: Lohse and Smetana, 1985:281, 293.

*Diagnosis.* *Lypoglossa angularis* is practically indistinguishable externally from *L. franclemonti*. Adults, however, differ from those of the latter species by having a more transverse pronotum with rather pronounced, obtuse posterior angles (Fig. 7). Moreover, the pronotal color is usually darker in *L. angularis*, and less contrasting with the head and elytra. The shape of the median lobe of the aedeagus (Figs. 15–16), and the apical lobe of the paramerite (Fig. 17) are the best diagnostic characters for identification of this species.

*Redescription.* Length 3.7–4.2 mm. Body color generally dark, reddish-brown, except mouthparts, antennae, legs, and oblique, indistinct band across each elytron often paler. Head and abdomen generally darker, piceous. Abdominal terga VI–VII usually with bluish-black iridescent sheen.

Head punctuation, setation, and microsculpture similar to that in *L. franclemonti*. Antennae slightly shorter, more robust than in *L. franclemonti*; articles 1–3 elongate; article 4 slightly longer than or subequal to its width; articles 5–7 short, quadrate; articles 8–10 tending to be more transverse; article 11 conical, pointed apically, subequal to articles 9 + 10.

Pronotum strongly transverse (L/W ratio = 0.69–0.71), posterior margin distinctly bisinuate, posterior angles broadly obtuse (Fig. 7). Integument distinctly imbricate, moderately glossy; pubescence with microsetae as in *L. franclemonti*.

Elytra and abdomen as in *L. franclemonti*.

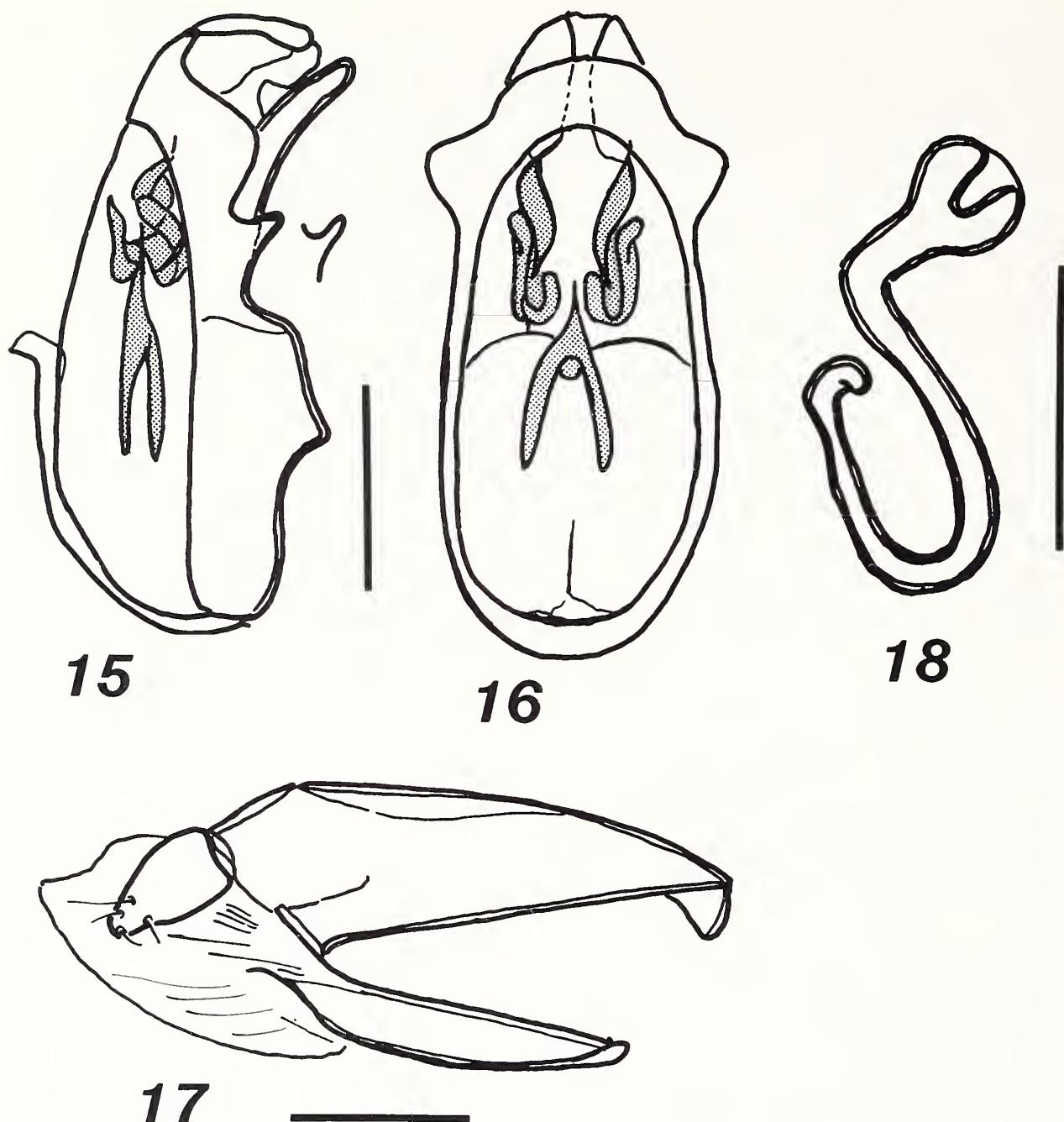
Male: Median lobe of aedeagus as in Figures 15–16. Paramere and apical lobe of paramerite as in Figure 17.

Female: Spermatheca as in Figure 18.

*Secondary sexual characteristics.* Male: Dorsum of head, and narrow median strip of pronotum impressed. Female: Dorsum of head and pronotum usually evenly convex (sometimes narrow, median line finely impressed).

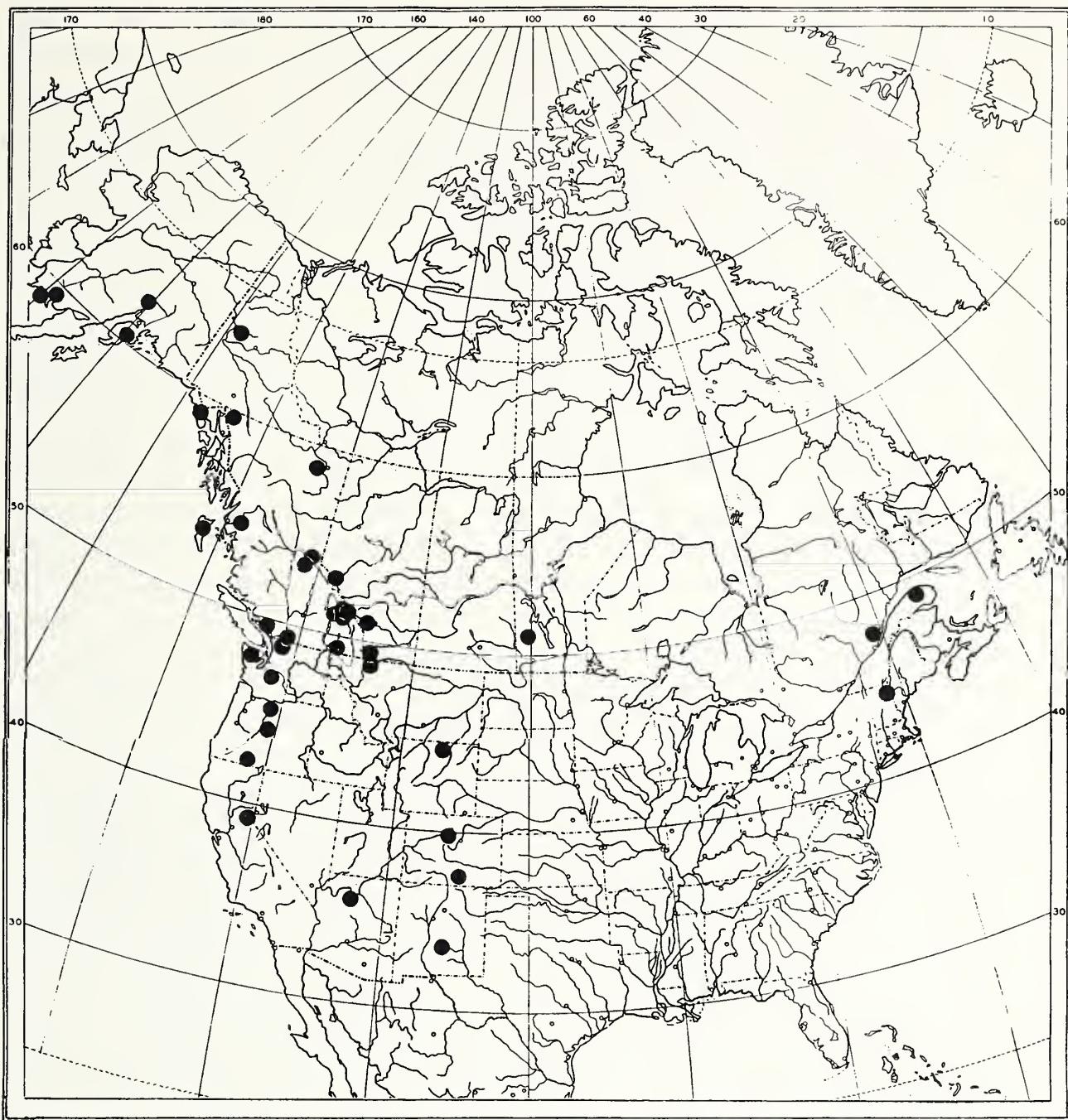
*Geographic distribution.* *Lypoglossa angularis* is widely distributed in northwestern North America (Alberta, British Columbia, Yukon Territory, Manitoba, and Alaska), with relict populations on the higher mountains in the Gaspe, eastern Quebec, and northern New Hampshire, and in the high elevations of northern California, Oregon, Washington, Colorado, New Mexico, Arizona, Wyoming, and Montana (Map 2).

*Material examined.* (1,087 specimens): CANADA: Alberta: Banff, 6-VI-1924 (CASC, 6); Banff, Dr A Fenyes (FMNH, 1). Banff N.P., Boom Lk., 6,000 ft, 16-VII-1971,



Figs. 15–18. *Lypoglossa angularis*. 15, Median lobe of aedeagus, lateral aspect; 16, Median lobe of aedeagus, dorsal aspect; 17, Paramere; 18, Spermatheca (Glacier, British Columbia). (Scale line = 0.25 mm)

JM & BA Campbell (CNCI, 11); Bow Lk., 16-VI-1968, 6,500 ft, Campbell & Smetana (CNCI, 4); Agnes Lk., 7,000 ft, 17-VII-1971, JM Campbell (CNCI, 2); Consolation Lk., 64–7,000 ft, 15-VI-68, Campbell & Smetana (CNCI, 26); Cirrus Mt., 5,500 ft, 16-VI-1968, Campbell & Smetana (CNCI, 1); Smith Lk., 15-VII-1971, JM & BA Campbell (CNCI, 1); Mt. Temple Ski Lodge, 6,600 ft, 12-VIII-1971, JM Campbell (CNCI, 1). Jasper N.P., Mt. Edith, Cavell, 6,000 ft, 22-VIII-1971, JM Campbell (CNCI, 1). Kananaskis F.E.S., Lusk Creek, 14-VII-1971, JM & BA Campbell (CNCI, 31); 2.5 mi SE Kananaskis, F.E.S., 15-VIII-1970, EE Lindquist (CNCI, 2); 10 mi SW Kananaskis F.E.S., Marmot Creek Basin, 6,500 ft, 13-VII-1971, JM & BA Campbell (CNCI, 19). Waterton Lks. N.P., Crypt Lake, 6,500 ft, 22-VI-1980, JM Campbell



Map 2. Known geographic distribution of *Lypoglossa angularis*.

(CNCI, 1); Crypt Lk. Tr., 4,900 ft, 23-VI-1980, JM Campbell (CNCI, 1); Lower Bertha Falls, 4,800 ft, 10-VI-1980, JM Campbell (CNCI, 3); Bertha Creek, 49–5,800 ft, 10-VI-1980, JM Campbell (CNCI, 5); Summit-Carthew Lks. Tr., 7,000 ft, 17-VI-1980, JM Campbell (CNCI, 3). Lower Waterton Lk., 4,500 ft, 26-VI-1980, JM Campbell (CNCI, 1); Cameron Cr., 5,200 ft, 24-VI-1980, JM Campbell (CNCI, 7); Cameron Lk., 8–9-VI-1980, 9–14-VI-1980, 17–19-VI-1980, 5,450–5,500 ft, JM Campbell (CNCI, 19); Cameron Lake, 5,500 ft, 31-VII-1980, DE Bright (CNCI, 1); Cameron Lake, 7.VI.1980, 8–11-VI-1980, 23-VI-1980, IM Smith (CNCI, 4); Cameron Ck. picnic ground, 12–16-VI-1980, 17–28-VI-1980, 5,350 ft, IM Smith (CNCI, 29); Rowe Lks. Tr., 5,300–6,500 ft, 7–15-VI-1980, JM Campbell (CNCI, 48); Mother Duck Tr. above Cameron Lk., 17-VI-1980, IM Smith (CNCI, 9); Mother Duck Tr., 58–6,200 ft, 17-VI-1980, JM Campbell (CNCI, 11); Crandell Lk., 19-VI-1980, 5,000

ft, JM Campbell (CNCI, 11); Crandell Lk. Tr., 13-VI-1980, IM Smith (CNCI, 11); Little Prairie picn. area, 23-VI-1980, I Smith (CNCI, 2); Rowe Creek, 5,300–5,500 ft, 7-VI-1980, 21-VI-1980, 4-VIII-1976, JM Campbell (CNCI, 14); Rowe Cr. Tr., 60–6,300 ft, 15-VI-1980, JM Campbell (CNCI, 4); Rowe Trail, 6,400 ft, 16-VI-1980, JM Campbell (CNCI, 4). *British Columbia*: Em[era]ld Lake, 6-VI-1927 (CASC, 2). Glacier, Dr. A Fenyes (CASC, MCZC, FMNH, AMNH, 23). Manning Prov. Pk., Mt. Frosty, 6,100 ft, 30-VII-1975, JM & BA Campbell (CNCI, 1); Blackwell Pk., 6,000–6,750 ft, VI-20-1968, Campbell & Smetana (CNCI, 26); Blackwell Peak, 3,000 ft, V-31-1968, Campbell & Smetana (CNCI, 6). 8 mi W, 21 mi W Creston, 10-VI-1968, 9-VI-1968, Campbell & Smetana (CNCI, 3). Slide Mt., 10 mi E Barkerville, 4,500 ft, 23–24-VI-1968, Campbell & Smetana (CNCI, 25). Kootenay N.P., Kimpton Cr., 4,000 ft, 21-VII-1971, JM & BA Campbell (CNCI, 7); Sinclair Cr., 6,000 ft, 12-VI-1968, Campbell & Smetana (CNCI, 22). Yoho N.P., Lk. McArthur, 7,000 ft, 28-VII-1971, JM & BA Campbell (CNCI, 4); Valley of Hagen Peak, 6-VIII-1971, JM & BA Campbell (CNCI, 1); Lk. O'Hara, 6,700 ft, 30-VII-1971, JM & BA Campbell (CNCI, 6); Otterhead R., 5,500 ft, 3–7-VIII-1971, JM Campbell (CNCI, 38); Amiskwi R., 6,000 ft, 5-VIII-1971, JM & BA Campbell (CNCI, 4). Mi 56 Haines Hwy., 3 Guardsmen Pass, 4-VII-1968, 3,200 ft, Campbell & Smetana (CNCI, 26); Haines Hwy., km 143–144, 2,400 ft, 22-V-1978, Smetana & Becker (CNCI, 4). 5 mi E Whistler's Mt., 29-V-1968, Campbell & Smetana (CNCI, 28). Mt. Revelstoke N.P., 6,500 ft, 18-VIII-1971, JM & BA Campbell (CNCI, 1); Eva Lk., 6,500 ft, 25-VII-1971, JM & BA Campbell (CNCI, 61); Mt. Revelstoke, 6,000 ft, 8-VII-1952, GP Holland (CNCI, 2); Mt. Revelstoke, 6,300 ft, 18-VI-1968, Campbell & Smetana (CNCI, 7). 7.6 km E Hwy 25, 6.2 km S Terrace, Copper Mt. Rd., 24-VIII-1983, JM Campbell (CNCI, 1). 46 km W McBride, 26-VIII-1983, JM Campbell (CNCI, 1). Two Sisters Mt., 15 mi E Barkerville, 4,500–6,500 ft, 23–24-VI-1968, Campbell & Smetana (CNCI, 16). Courtney, Forbidden Plateau, nr Courtney Lookout, 25-VII-1979, IM Smith (CNCI, 4); Forbidden Plateau, McPhee Lake, 3,700 ft, 19-VII-1975, JM & BA Campbell (CNCI, 1). Garibaldi Prov. Pk., Diamond Head Tr., 4,000–4,500 ft, 26-VII-1973, A & Z & D Smetana (CNCI, 1); Opal Cone, 5,200 ft, 3-VIII-1975, JM & BA Campbell (CNCI, 1). Atlin, 2,200 ft, 23-VI-1955, H Huckel (CNCI, 1). Summit Lake, Mi 392 Alaska Hwy., 4,200 ft, 23-VIII-1959, RE Leech (CNCI, 1). Queen Charlotte Isl., Moresby Isl., Mt. Moresby, 2,100 ft, 25-VII-1983, JM Campbell (CNCI, 5). *Manitoba*: Riding Mt. N.P., 1 km SE Long Lake, 16-IX-1979, A Smetana (CNCI, 1); Stathclair Trail, 4.5 km S Kinnis Crk., 12-IX-1979, A Smetana (CNCI, 6). *Quebec*: Parc Gaspesie, Lac Cascapedia, 14-VII-1972, 1,700 ft, JM & BA Campbell (CNCI, 1); Mont Albert, 8-VII-1972, 1,000 ft, JM & BA Campbell (CNCI, 3); Mont Albert, 10-11-VII-1972, 2,800–3,700 ft, JM Campbell (CNCI, 8); Mt. Albert, 3,150 ft, 20-VI-1954, 2-VI-1954, GP Holland (CNCI, 9). Parc des Laurentides, Lac Arthabaska, 2,800 ft, 21–22-VIII-1970, JM & BA Campbell (CNCI, 3); Mare-du-Sault, 2,700 ft, 15–17-VIII-1970, JM & BA Campbell (CNCI, 4); Bois Verts, 2,800 ft, 18-VIII-1970, JM & BA Campbell (CNCI, 1). Mont Jacques, Cartier, 4,000 ft, 22-VII-1972, JM Campbell (CNCI, 4). *Yukon Territory*: Dempster Hwy., Mi 29.5, 2,800 ft, 24-VII-1978, JM Campbell & A Smetana (CNCI, 2); Mi 45, 3,500 ft, 14-VII-1968, Campbell & Smetana (CNCI, 4); Mi 42, N Klondike R., 3,300 ft, 18-VII-1978, Smetana & Campbell (CNCI, 14); Mi 53, North Fork Pass, 4,200 ft, 24-VII-1978, A Smetana & JM Campbell (CNCI, 1).

UNITED STATES: *Alaska*: 2.5 mi S Lituya Bay, Mount Blunt, 2,500 ft, VI/3-IX-1977, 4-VI-1977, 1-VII-1977, Dan Mann (AMNH, 70). 7.5 mi NNW Dillingham, Wood River Red Bluff,  $59^{\circ}8'30''$ ,  $158^{\circ}33'W$ , 18-VI-1980, L Herman (AMNH, 4). Hagemeister Island, North shore at base of long sand spit, 24-VI-1980,  $58^{\circ}38'N$ ,  $161^{\circ}04'30''W$ , L Herman (AMNH, 5). Kenai Pen., 3 mi SE Kenai, 7-VI-1978, Smetana & Becker (CNCI, 1); Kalifonsky Bch., nr Kenai, 8-VI-1978, Smetana & Becker (CNCI, 9); Clam Gulch, 6-VI-1978, Smetana & Becker (CNCI, 3); Hope, 12-VI-1951, WJ Brown (CNCI, 1); Nimilchik, 24-VI-1951 (CNCI, 1); Kasilof R. at Hwy. 1, 12-VI-1978, Smetana & Becker (CNCI, 1); 8 mi SE Kasilof, 9-VI-1978, Smetana & Becker (CNCI, 3); Anchor Riv. at Hwy, 450 ft, 4-5-VI-1978, Smetana & Becker (CNCI, 34); Anchor R. Cpgd., 12 mi N Homer, 450 ft, 5-VI-1978, Smetana & Becker (CNCI, 8). 12 mi N mi 78 Denali Hwy., Windy Cr., 13-VII-1978, Smetana & Campbell (CNCI, 1). Denali St. Pk., Byers Crk. at Hwy. 1, 20-VI-1978, Smetana & Becker (CNCI, 2); Byers Lk. Cpgd., 23-25-VI-1978, Smetana & Becker (CNCI, 49). Kenai Mts., 9 mi N Seward, 14-VI-1980, L Herman (AMNH, 7); 15 mi N Seward, 400 ft, 29-V-1978, Smetana & Becker (CNCI, 12); 16 mi N Seward, 500-600 ft, 26-V-1978, Smetana & Becker (CNCI, 2); 23 mi N Seward, 600-900 ft, 28-V-1978, Smetana & Becker (CNCI, 7); 22 mi N Seward, 600-800 ft, 27-V-1978, Smetana & Becker (CNCI, 30); Ptarmigan Ck. Cpgd., 500-600 ft, 26-V-1978, Smetana & Becker (CNCI, 9). Kenai Mts. Crk., above Tem Lk. Cpgd., 850-900 ft, 13-VI-1978, Smetana & Becker (CNCI, 52); same locality as preceding, except 850 ft, 16-VI-1978 (CNCI, 3). *Arizona*: Coconino Co., San Francisco Mtns., Mt. Agassiz, 3,200 m, 28-VII-1976, JM Campbell (CNCI, 2); Snow Bowl, 2,800 m, 27-VII-1976, JM Campbell (CNCI, 1); San Francisco Mts., Mann (CASC, FMNH, 3). *California*: El Dorado Co., L. Tahoe, Cascade Lk., 6,300 ft, 11-VIII-1969, A Smetana (CNCI, 1). Deer Park Inn, Dr. A Fenyes (MCZC, 3). Colorado: Huerfano Co., 15 mi SSW LaVeta, Cucharas Creek, 9,400 ft, 16-VIII-1982, L Herman (AMNH, 3). Grand Co., Rollins Pass, 11,000 ft, 5-VIII-1973, JM Campbell (CNCI, 1). Coal Bank Pass, 10,550 ft, 31-VII-1973, JM Campbell (CNCI, 3). Montana: Glacier Co., Glacier N.P., Logan Pass, 6,600 ft, 11-VII-1971, JM & BA Campbell (CNCI, 7). New Hampshire: Coos Co., Mt. Washington, 3,800 ft, 16-VIII-1976, JM & BA Campbell (CNCI, 3); above Lake of the Clouds, 6-VII-1914, CA Frost (CASC, 1); Mt. Wash[ington] (CASC, 5). Randolph, 18-IX-1909 (CNCI, 1). Starr Lake, 4,890 ft (CASC, 1). New Mexico: Lincoln Co., Sierra Blanca, 11,500 ft, 18-VII-1969, A Smetana (CNCI, 5); Sierra Blanca Ski Area, 10,600 ft, 18-VII-1969, A Smetana (CNCI, 2). Oregon: Deschutes Co., 12 mi SW Sisters, FSR 1551, 4,400 ft, 23-VII-1979, JM & BA Campbell (CNCI, 1). Hood River Co., Mt. Hood, Cloud Cap Rd., Tilly Jane Crk., 4,100 ft, 30-VI-1974, A & D Smetana (CNCI, 8). Klamath Co., Cold Spring Camp, 33 mi NW Klamath Falls, 5,800 ft, 22-VI-1978, J Schuh, L & N Herman (AMNH, 3). Wasco Co., 19 mi WNW of Dufur, Wampus Springs, 4,800 ft, 9-VII-1978, L & N Herman (AMNH, 1). Washington: Clallam Co., Olympic N. P., 13 mi S Port Angeles, 4,000 ft, 11-VIII-1979, JM & BA Campbell (CNCI, 1). Pierce Co., Mt. Ranier N.P., N Puyallup River, 3,700 ft, 10-VIII-1973, A & Z & D Smetana (CNCI, 2); Sunbeam Falls, 4,000 ft, 17-V-1968, Campbell & Smetana (CNCI, 2). Whatcom Co., Mt. Baker, 4 mi N Silver Fir Camp, 4,000 ft, 16-VIII-1975, JM & BA Campbell (CNCI, 7). Wyoming: Sheridan Co., 27 mi WSW Ranchester, Big Horn Mts., nr Prune Creek Campgd., South Tongue River, 7,700 ft, 25-26-VIII-1982, L Herman (AMNH, 17).

*Bionomics.* Very little is known about the habits of this species. Some Alberta and British Columbia specimens were taken in sifted moss and liverworts, and from sifted alder, *Populus*, willow, spruce, Douglas fir, and Lodgepole pine litter. Other specimens bear the following habitat data: "human dung trap, mouse nests, gopher burrows, pitfall edge meadow, sifting bear dung, river debris, under bark, sifting pile of squirrel midden, dung pan traps," and "horse dung." Most specimens have been taken in May, June, July, and August, and occasionally in September.

*Remarks.* Male and female genitalia of *L. angularis* are accurately figured in Lohse and Smetana (1985, Figs. 19–21, p. 295). The above authors also mentioned the presence of "1 specimen [of *L. angularis*] from Newfoundland" in the Canadian National Collection (CNCI). I did not examine any CNCI specimens of *L. angularis* collected from Newfoundland, but the distributional record would not surprise me.

### *Lypoglossa lateralis* (Mannerheim)

*Oxypoda lateralis* Mannerheim, 1830:70.

*Megacrotona lateralis*: Benick and Lohse, 1974:103.

*Lypoglossa lateralis*: Lohse & Smetana, 1985:294.

In the course of examining specimens for this taxonomic study of *Lypoglossa*, I had the opportunity to examine type specimens (syntype series) of *L. lateralis* (Mannerheim), the only known Palearctic representative of this holarctic genus. As a result, it seems appropriate and warranted to designate a lectotype here.

The original syntype series in the Mannerheim collection, Zoological Museum, University of Helsinki, Finland, consists of 4 pinned specimens (see Silfverberg, 1988). I examined all specimens of the series. They are labeled as follows: *Spec. No. 1*: [red triangle] = Villnas, Finland (a manor some 30 km NW of Turku/Abo)/"Abo"/"Coll. Mannh."/ "Spec. typ."/ "108"/[red square]/"Mus. Zool. H:fors Spec. typ. No. 211 Oxypoda lateralis Mann." *Spec. No. 2*: [red triangle]/"Abo"/"Coll. Mannh."/ "Spec. typ."/ "109"/[red square]/"Mus. Zool. H:fors Spec. typ. No. 212 Oxypoda lateralis Mann." *Spec. No. 3*: [red triangle]/"117." *Spec. No. 4*: [red triangle] only.

Specimen No. 1 bearing the label "Spec. typ. No. 211" is hereby designated as lectotype (sex undetermined, undissected) of *Oxypoda lateralis*; the label LECTOTYPE Oxypoda lateralis Mann., design. 1991, E. R. Hoebeke, is attached. Specimen No. 4, male, bearing only a small [red triangle] label, was dissected and remounted on a small cardboard placard; the aedeagus is mounted in a drop of Hoyer's medium on the card. The label PARALECTOTYPE Oxypoda lateralis Mann., design. 1991, E. R. Hoebeke, is attached to Specimen Nos. 2–4 of the syntype series.

### ACKNOWLEDGMENTS

Specimens used in this study were borrowed from several institutional and university collections, and I gratefully acknowledge the assistance of the curators responsible. The abbreviations listed below refer to material mentioned in the text.

American Museum of Natural History, New York (AMNH), L. H. Herman  
California Academy of Sciences, San Francisco (CASC), D. H. Kavanaugh  
Canadian National Collection, Ottawa (CNCI), J. M. Campbell  
Cornell University Insect Collection, Ithaca, NY (CUIC)

Field Museum of Natural History, Chicago (FMNH), A. F. Newton, Jr.  
Museum of Comparative Zoology, Cambridge, MA (MCZC), D. G. Furth  
Snow Entomological Museum, University of Kansas, Lawrence, KS (SEMC), J. S. Ashe  
University of Vermont, Burlington, VT (UVCC), R. T. Bell  
University of New Hampshire, Durham, NH (DENH), D. S. Chandler  
Zoological Museum, University of Helsinki, Finland (UZMH), H. Silfverberg

I also appreciate the assistance given by Herbert Främbbs, a visiting German scholar (University of Bremen) studying at Cornell University, who donated staphylinids to the Cornell collection that included specimens of *Lypoglossa* collected from bogs in Maine. The loan of type specimens was made possible by H. Silfverberg (Zoological Museum, University of Helsinki, Finland) and A. F. Newton, Jr. (Field Museum of Natural History, Chicago), and special thanks are due to these individuals. I acknowledge my colleagues James K. Liebherr and Quentin D. Wheeler for helpful suggestions and for editing the manuscript, and J. Howard Frank (University of Florida, Gainesville) and J. S. Ashe (Snow Entomological Museum, University of Kansas, Lawrence) also provided valuable criticism of the manuscript.

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THE NEW WORLD **BLEPHARIDA** GROUP, WITH A KEY TO  
GENERAL AND DESCRIPTION OF A NEW SPECIES  
(COLEOPTERA: CHRYSOMELIDAE)

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*Abstract.*—Using external and internal adult morphology, clarification of status and determination keys are provided for *Blepharida* Chevrolat and the eight New World genera either related to it or placed near it in recent catalogues. The morphological reasons (e.g., pattern) for maintaining *Blepharida* and *Notozona* Chevrolat as separate genera are discussed. The Afro-tropical genus *Blepharidina* Bechyné is lowered to subgenus status within the genus *Blepharida* in light of morphological similarities and differences with New World *Blepharida*. *Blepharida haitiensis* Blake is transferred to *Acrocyum* Jacoby. Morphological evidence (e.g., metatibial emargination, eye shape, and metafemoral spring shape) for placing the monotypic *Euplectroscelis* Crotch close to *Blepharida* is given. *Blepharida franclemonti* is described as a new species known to date only from the Yucatan Peninsula of Mexico.

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In the catalogue-like checklist of Leaf Beetle genera of the world followed by most workers (Seeno and Wilcox, 1982), the Alticinae (Chrysomelidae) begin with a group of three genera, formerly Galerucinae (Decarthrocerini of Laboissiere, 1937). This group is followed by three groups of genera that are confused in keys and collections. The first of these groups consists of three Neotropical genera (*Elithia* Chapuis, *Procalus* Clark—originally in Galerucinae, and *Crimissa* Stål). The second group consists of 14 genera from around the world, including 7 found in the New World (Nearctic and/or Neotropical): *Blepharonycha* Fall; *Blepharida* Chevrolat; *Chrysogramma* Jacoby; *Acrocyum* Jacoby; *Notozona* Chevrolat; *Pseudorthygia* Csiki; and *Phydanis* Horn. The third group contains only two Afrotropical genera (*Diamphidia* Gerstaecker and *Polyclada* Chevrolat) which probably should be combined with the previous group. As stated by Seeno and Wilcox (1982), these groups (family-groups) are quite artificial and should not be considered as accepted groupings or tribal arrangements. Unfortunately the separation of these family groups in the Seeno and Wilcox (1982) checklist and their indication of nominate genera for most of these groups is very misleading and has caused some authors to refer to these family-groups incorrectly as tribes. In the present paper the author will attempt to clarify some morphological relationships among the New World genera of the above-mentioned family-groups surrounding the genus *Blepharida*.

Morphological relationships of most of these New World *Blepharida* relatives are apparent in Scherer's 1983 key to the Neotropical Alticinae (a translation of Scherer, 1962); *Pseudorthygia* and *Phydanis*, considered by Scherer to be Nearctic, were not included; however, these two genera are included in Arnett's (1971) keys to North American Alticinae. The genus *Euplectroscelis* Crotch is not included in Arnett (1971) or Scherer (1983), even though in Wilcox (1975) it is placed next to the *Blepharida*-related genera. The relationships of some of these genera have been questioned by

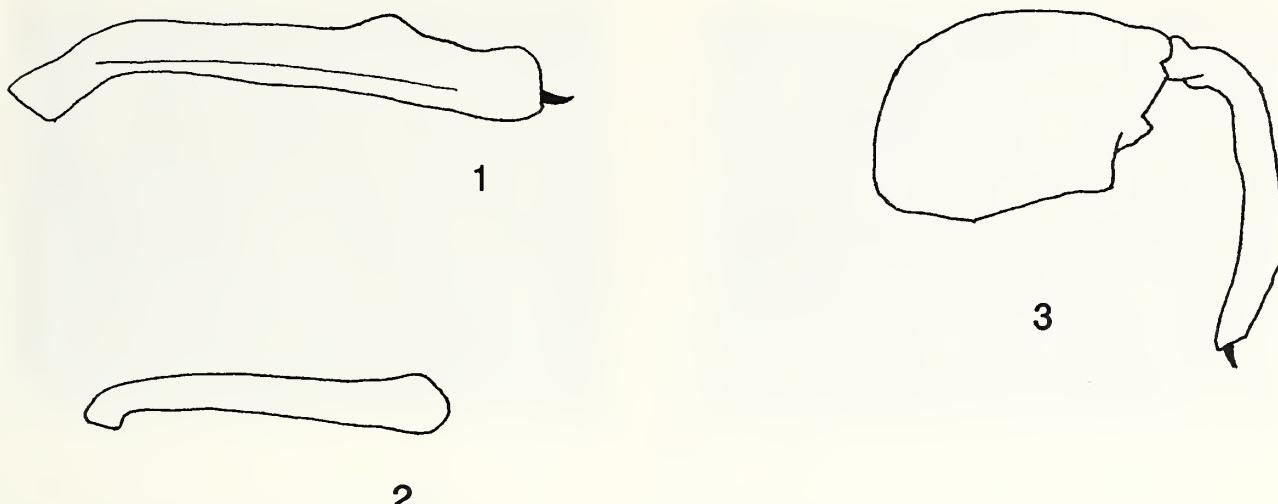
several workers. Bechyné (1968) considered the genera of the second family-group from Seeno and Wilcox (1982) to be the Blepharidini. He disagreed with Scherer's (1961) interpretation of the genus *Blepharida* as including the New World *Blepharida* (*sensu stricto*) together with the Old World *Calotheca* Heyden and *Blepharidella* Weise. Bechyné (1968) argued that chaetotaxy and other morphological details of the clypeus and the tarsal claws were good reasons for leaving these all as separate genera. Based on the presence of a transverse series of setiferous punctures along the anterior border of the clypeus and the absence of a transverse depression in the clypeus (forming a carina above), Bechyné (1968) claimed that only three species (*B. rhois* Forster, *B. irrorata* Chevrolat, and *B. haitiensis* Blake) formed the true *Blepharida* and that all other New World *Blepharida* were congeneric with *Notozona*.

Bechyné (1968) then created a new genus (*Blepharidina*) to encompass all non-New World *Blepharida*, i.e., Afrotropical and Madagascan, possessing bifid tarsal claws, closed procoxal cavities, prosternum with a non-emarginate apex, and a pro-epimeron separated at its lateral border by a deep groove from the edge of the pronotum. Bechyné (1968) considered *Blepharonycha* to be a valid genus because, although it shares the character of bifid tarsal claws with *Blepharida* and *Notozona*, it differs by having open procoxal cavities. He also considered *Acrocymum* to be congeneric with *Chrysogramma* which he wrote had appendiculate tarsal claws but variable procoxal cavities.

New World species of *Blepharida* and *Notozona* are very difficult to separate using the morphological characters used in traditional dichotomous keys. Baly (1865) separated these two genera using several characters which were not true for all species, especially the subapical tooth on the dorsal edge of the metatibiae (*Blepharida*) and the more swollen metafemora with a ventral tooth of *Notozona*. Chapuis (1875) separated these genera using the maxillary palps; narrow and filiform in *Blepharida* versus robust and claviform in *Notozona*. However, none of these or other single morphological characters work for separation of all species in these two genera, as pointed out by Jacoby (1885). Jacoby (1885, 1891) stated that because he could not find any structural differences between these two genera, *Notozona* might be included with *Blepharida*, but he still kept them as separate genera based on consistent color pattern differences. Scherer (1983) acknowledges Bechyné's (1968) treatment of *Blepharida*, but offers his opinion that the true *Blepharida* includes one Nearctic species [*B. rhois*] and many of the Afrotropical species. In his 1983 keys, Scherer stated that it is too early for him to form an opinion about the Neotropical species, but that many belong to *Notozona*. Although Scherer mentions several places in his 1983 keys the potential for confusing *Blepharida* and *Notozona*, he nevertheless does separate and list them based on the deep transverse impression in the anterior part of the frons. Most of Scherer's (1983) characters for separating *Blepharida* and *Notozona* from other genera seem to be based on description of Afrotropical *Blepharida*.

#### METHODS

Specimens including types were borrowed from a variety of institutions (see Acknowledgments). The metafemoral spring (a generic-level character) was studied for all the genera concerned using the methods described in Furth (1989) (see also Furth, 1985, 1988). In addition, the female spermatheca and male aedeagus were studied



Figs. 1-3. 1. *Blepharida mexicana* metatibia (Length = L = 2.89 mm). 2. *Notozona histrio* metafemur (L = 3.55 mm) and metatibia (L = 3.37 mm). 3. *Elithia* sp. metatibia (L = 3.96 mm).

in more than one species of each genus whenever possible. These genitalic structures were extracted after prolonged heating (not boiling) of entire specimens in water. All dissections were made with Wild M5 stereomicroscope, including a calibrated reticle and camera lucida attachment. All photographs were made with a Wild M 400 Photomakroskop using Kodak TMAX 400 film.

Types of all the described species of New World *Blepharida* (*sensu lato*) and of *Notozona* have been studied by the author. Examples of three of the five described species each of *Elithia* and *Crimissa* and the two valid species (I. Askevold, personal communication) of *Procalus* were also examined. In addition the following number of species (of the known described species) were examined for this study: *Blepharonycha* (1 of 1); *Chrysogramma* (4 of 5); *Acrocyum* (2 of 4); *Euplectroscelis* (1 of 1); *Pseudorthygia* (1 of 2); and *Phydanis* (1 of 2).

#### KEY TO THE GENERA OF THE NEW WORLD BLEPHARIDA-GROUP

1. Apex of metatibia with dorsal edges emarginate or flattened (Figs. 1, 2); eyes oriented dorso-mesally, elliptical-shaped, large (dorso-ventral length equal to or greater than the dorsal interocular distance) (Fig. 4); metafemoral spring without recurve flange from ventral lobe, with an acute basal angle of ventral lobe, and with a long dorsal lobe extended arm (Fig. 8) [*Phydanis* has the first but not the second and third of the three characters listed above] ..... 2
- 1'. Apex of metatibia not emarginate or flattened, but with continuous, morphologically unchanged dorsal edges (Fig. 3); eyes round, not oriented dorsally towards each other, small (diameter usually considerably less than interocular distance) (Figs. 5, 6, 7); metafemoral spring with different morphology than Figure 8, most (except *Acrocyum* and *Pseudorthygia*) with basal angle of ventral lobe obtusely angled or with recurve flange (Figs. 9, 10, 11, 12, 13, and 16—metafemoral spring morpho-groups #1 and #3, respectively, see Furth, 1989) ..... 5
2. Tarsal claws simple ..... *Euplectroscelis*
- 2'. Tarsal claws appendiculate ..... *Phydanis*
- 2''. Tarsal claws bifid ..... 3
3. Procoxal cavities open ..... *Blepharonycha*



4



6



5

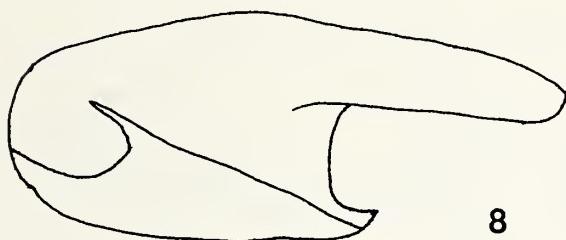


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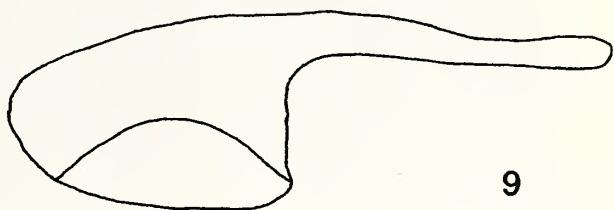
Figs. 4–7. 4. *Blepharida franclemonti* face and eyes (interocular distance dorsally = 1.04 mm). 5. *Procalus mutans* face and eyes (interocular distance = 1.18 mm). 6. *Crimissa cruralis* face and eyes (interocular distance = 1.78 mm). 7. *Chrysogramma pictipennis* face and eyes (interocular distance = 0.85 mm).

(*Blepharida flavocostata* keys to here, but has 6 thin, longitudinal stripes (costae) on non-striate elytra)

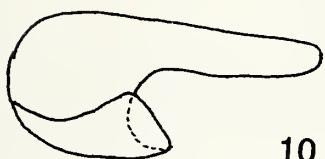
- 3'. Procoxal cavities closed (even very narrowly) ..... 4
- 4. Elytral pattern mottled (irregular/variable, sometimes asymmetrical; one species, endemic to Baja California [Mexico] has all black elytra) (Figs. 23, 24, 25), occasionally with vague irregularly bordered, transverse bands or series of small/tiny light-colored spots; metatibial apex emarginated with a preapical tooth or protuberance on outer dorsal edge (Fig. 1); elytral punctures usually not striate (arranged in rows), but with some exceptions (e.g., *B. rhois*); clypeus (lower frons) often flat or only slightly impressed transversely; metafemur without ventral subapical teeth; metatibia not strongly curved ..... *Blepharida*
- 4'. Elytral pattern with distinct (large/wide) transverse bands or spots, variable in size, but never mottled (Figs. 26, 27, 28); metatibial apex with dorsum flattened, but not emarginate and without preapical protuberance (Fig. 2); elytral punctures striate, sometimes appearing as double puncture rows, punctures fine and close together; clypeus (lower frons) usually with a deep transverse impression; metafemur often with a subapical, ventral tooth and with metatibia strongly curved, especially in males (Fig. 2) ..... *Notozona*



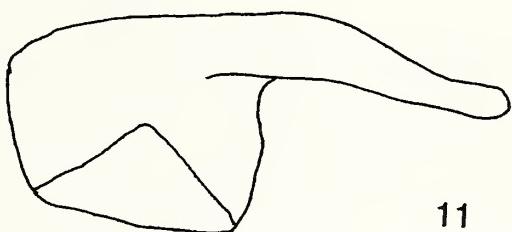
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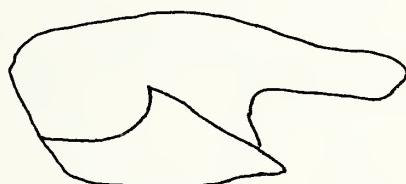
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10



11



12

Figs. 8–12. 8. *Blepharida mexicana* metasternal spring ( $L = 1.23$  mm). 9. *Elithia* sp. metasternal spring ( $L = 1.41$  mm). 10. *Procalus mutans* metasternal spring ( $L = 0.81$  mm). 11. *Crimissa cruralis* metasternal spring ( $L = 1.15$  mm). 12. *Pseudorthygia nigritarsis* metasternal spring ( $L = 0.41$  mm).

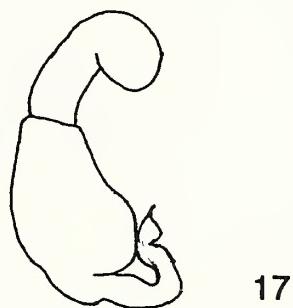
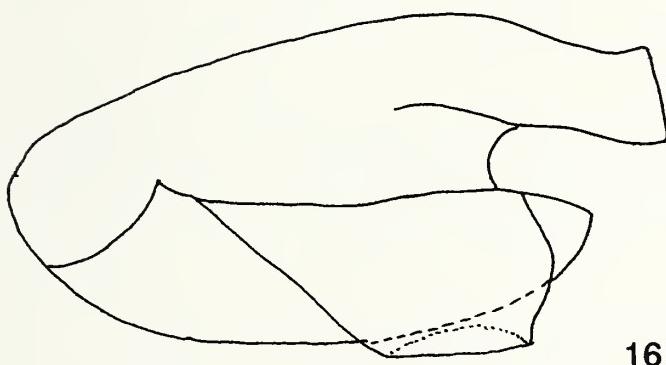
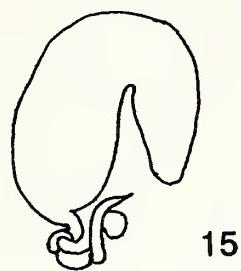
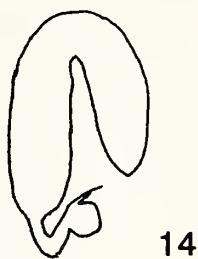
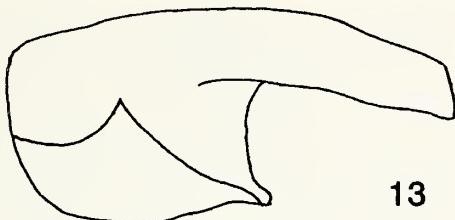
- |  |                 |
|--|-----------------|
| 5. Tarsal claws bifid .....  | 6               |
| 5'. Tarsal claws simple .....  | 7               |
| 5". Tarsal claws appendiculate .....   | 8               |
| 6. Procoxal cavities open; metasternal spring with basal angle of ventral lobe somewhat obtuse (ca. $100^\circ$ ) (Fig. 10); body smaller (size 6–10 mm) and elongate oval in shape .....                  | <i>Procalus</i> |
| 6'. Procoxal cavities closed; metasternal spring with basal angle of ventral lobe obtuse (more than $120^\circ$ ) (Fig. 9); body larger (9–15 mm) and more spherical in shape .....                        | <i>Elithia</i>  |
| 7. Procoxal cavities closed; metasternal spring with basal angle of ventral lobe obtuse (Fig. 11); body larger (9–15 mm); elytral punctuation confused; distributed in South America north to Panama ..... | <i>Crimissa</i> |
| 7'. Procoxal cavities open; metasternal spring with basal angle of ventral lobe acute (Fig.  |                 |

- 12); body smaller (ca. 4 mm); elytral punctuation striate; distributed in Mexico ..... *Pseudorthygia*
8. Metatibial apex with dorsal edges flattened (Fig. 2); body smaller (3–4 mm); elytral punctuation striate; elytral color solid blue/black (no pattern) ..... *Phydanis*
- 8'. Metatibial apex with dorsal edges continuous and morphologically unchanged (Fig. 3); body larger (4–8 mm); elytral punctuation confused; elytra with distinct pattern of large dark spots or transverse bands on a light background ..... 9
9. Procoxal cavities open (almost closed, but not); metafemoral spring with recurve flange from ventral lobe (morpho-group #3, see Furth, 1989) (Fig. 16); spermatheca with distinctly separate pump and receptacle and with spermathecal ductus simple and uncoiled (Fig. 17) ..... *Chrysogramma*
- 9'. Procoxal cavities completely closed; metafemoral spring (Fig. 13) without recurve flange from ventral lobe (morpho-group #1); spermatheca without distinctly separate pump and receptacle and some species with a coiled spermathecal ductus (Fig. 14, 15) ..... *Acrocyum*

#### RESULTS AND DISCUSSION

Admittedly the separation of *Blepharida* from *Notozona* is difficult. The combination of characters given in the key above should provide adequate means for separation of these two genera. Generally the reliance on color or pattern as a primary key character is not advisable; however, at present it appears to be the best possibility for these taxa. A variety of characters has been suggested for separation of *Blepharida* and *Notozona* by previous workers, but most have not proved 100% applicable. Therefore, it seems most practical to include several characters that each pertain to a majority of the species in each genus, the combination of which will yield almost complete reliability of determination. Some previous workers have also used a few other less reliable characters such as: antennal segment 2 distinctly shorter than segments 3 or 4 in *Blepharida*, whereas segments 2–4 subequal but shorter than the others in *Notozona*; and maxillary palpus narrow and filiform in *Blepharida*, but more robust/swollen and claviform apically in *Notozona*. These characters are of some use for separation of these two genera, but are quite variable in certain species. Further knowledge of the biology (e.g., Furth, 1982), foodplants, larvae, and other biological information may provide additional characteristics for the separation of *Blepharida* and *Notozona*. Preliminary information indicates that certain species in these genera feed on related foodplants (Furth, unpubl. data); however, foodplant preference testing, leaf biochemical differences, and even foodplant ecology may be useful for indicating relationships (Furth and Young, 1988). Also, the status of several species of *Blepharida* and *Notozona* will be changed in a species-level revisionary study of these two genera (Furth, unpubl. data). Therefore, the author prefers at this point to consider *Blepharida* and *Notozona* as valid separate genera in much the same way as Jacoby (1885, 1891) and Scherer (1983).

Bechyné (1968) states that the true *Blepharida* consisted of only three species based on a transverse series of setiferous punctures on the anterior clypeus and the absence of a transverse clypeal groove (with accompanying carina above). However, the author finds these characters present only in *B. rhois*, not in *B. irrorata* or *B. haitiensis*. In fact, the status of the last of these species is quite different, as discussed below. Bechyné (1968) lumped all other New World *Blepharida* (*sensu lato*) into *Notozona*; the present author disagrees and retains them as *Blepharida*.



Figs. 13–17. 13. *Acrocyum haitiensis* metafemoral spring ( $L = 0.56$  mm). 14. *Acrocyum haitiensis* spermatheca ( $L = 0.59$  mm). 15. *Acrocyum maculicollis* spermatheca ( $L = 0.59$  mm). 16. *Chrysogramma pictipennis* metafemoral spring ( $L = 0.85$  mm). 17. *Chrysogramma pictipennis* spermatheca ( $L = 0.70$  mm).

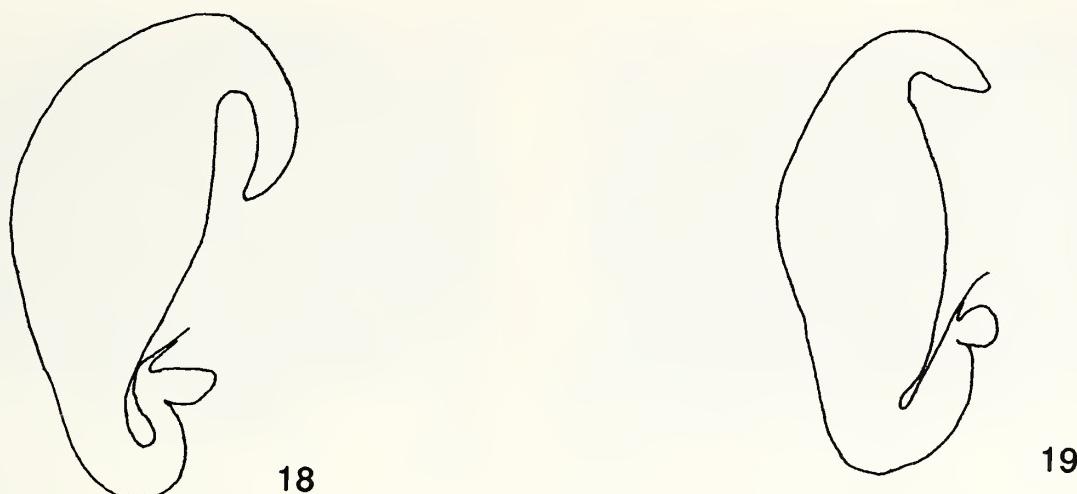
In the present study the aedeagus, spermatheca, and metafemoral spring of several species of both *Blepharida* and *Notozona* are studied to look for generic level characteristics. The aedeagi of these two genera are quite variable at the species level and show no generic level characters. The spermathecae of *Blepharida* and *Notozona* are quite similar in the shape of the main body of the spermatheca—receptacle and pump (Figs. 19, 18, respectively), but they do show some species differences in the ductus shape. The metafemoral spring of *Blepharida* and *Notozona* is essentially identical belonging to metafemoral spring morpho-group #1 (see Furth, 1988, 1989)—a long extension (extended arm) of the dorsal lobe, the ventral lobe without a recurved flange and with an acute basal angle (pointed basally) (Fig. 8). These three internal characters (aedeagus, spermatheca, and metafemoral spring) were also examined for

all the genera included in this study to reveal generic level characters. The results of this are partially reflected in the above key and the associated figures. As with *Blepharida* and *Notozona*, the aedeagus reveals little obvious definitive, generic level characters; however, a more comprehensive survey of species in these genera is needed in order to be certain of this conclusion. The spermatheca and metafemoral spring are much more revealing as generic characters, as demonstrated in the above key.

As indicated in the Introduction, there has been some confusion and disagreement as to the proper inclusions for the genus *Blepharida*. Scherer (1961) basically followed the catalogue arrangement of Heikertinger and Csiki (1940) which was continued by Seeno and Wilcox (1982). These authors considered *Blepharida* to be composed of three subgenera: *Blepharida* (*sensu stricto*), from the New World, possessing bifid tarsal claws; *Calotheca*, from East and South Africa and the Celebes, with simple tarsal claws; and *Blepharidella*, from East and South Africa, with appendiculate tarsal claws. Bechyné (1968) raised these subgenera to generic status, divided New World *Blepharida* into *Blepharida* (*sensu stricto*) and *Notozona*, and created a new genus, *Blepharidina*, for the Afrotropical species with bifid tarsal claws. Seeno and Wilcox (1982) treat *Blepharidina* as a valid genus. In the present study it has become apparent that there is a group of external morphological differences between the Afrotropical and New World *Blepharida* that possess bifid tarsal claws, other than those mentioned by Bechyné (1968). The author considers Bechyné's *Blepharidina* to be only a subgenus of *Blepharida* from the Afrotropical and Madagascan Regions, with bifid tarsal claws and possessing the following external morphological characters: proepimeron laterally separated from pronotum by a deep groove or suture; frons with deeply impressed, sinuate grooves extending from lower to upper frons between antennae; pronotum with antero-lateral quadrants with a short row of sublateral, longitudinal punctures, usually connected to a transverse (horizontal) row of coarse punctures reaching the lateral pronotal border, thus forming a square or circle in the antero-lateral corners of the pronotum; elytra always striate; clypeus without transverse groove or carina; anterior border of clypeus without transverse series of setiferous punctures; elytral epipleuron with some relatively large, dark spots/pattern of color. Preliminary examination also indicates some characteristic differences of spermathecal morphology (e.g., relatively longer pump). These characters, or at least in combination, are not present in the New World subgenus *Blepharida* (*sensu stricto*).

Another change in status is *Blepharida haitiensis* Blake, considered to be a true *Blepharida*, especially by Bechyné (1968). The following characters place *B. haitiensis* as a species of *Acrocyum*: form of the metafemoral spring (Fig. 13); female spermathecal morphology (Fig. 14); male aedeagus short and stout in form; absence of any flattening or emargination of the dorsum of the metatibial apex; appendiculate tarsal claws; small round eyes; elytral pattern primarily composed of dark spots; and elytral punctuation confused, very fine, sparse. Even though Bechyné (1968, unpubl. data) considered *Acrocyum* congeneric with *Chrysogramma*, evidence (i.e., metafemoral spring and female spermatheca) provided in the key above proves that they are truly separate genera.

The genus *Euplectroscelis* Crotch is a monotypic genus endemic to Baja California (Mexico). The six species described by Baly as *Euplectroscelis* and listed in Heikertinger and Csiki (1940) all belong to *Heikertingerella* Csiki. E. Riley and A. Gilbert (personal communication) have observed *Euplectroscelis* in nature. They report that



Figs. 18–19. 18. *Notozona histrionica* spermatheca ( $L = 1.22$  mm). 19. *Blepharida franclemonti* spermatheca ( $L = 1.04$  mm).

this and a *Blepharida* species feed on *Bursera* (Burseraceae) and that their larvae are similar morphologically and behaviorally to those of *Blepharida*. As indicated in the above key, the present study has revealed that *Euplectroscelis* adults are morphologically very similar to *Blepharida*, and that the placement of *Euplectroscelis* in catalogues or checklists should be just after *Blepharida* rather than far away near *Chaetocnema* Stephens as it is in Seeno and Wilcox (1982).

The author finds it curious that the arrangement of scientific names in catalogues or checklists (e.g., Heikertinger and Csiki, 1940, Seeno and Wilcox, 1982) is supposedly based on some type of similarities, presumably morphological; however, these similarities or the rationale of such catalogue arrangements is not explained or referred to and such "accepted" arrangements are often passed down through several generations. Admittedly, these traditional "catalogue phylogenies" are often convenient for curating collections and some doubtlessly reflect valid relationships; however, they must be viewed with great caution and restraint when inferring true phylogeny or broad-spectrum relationships. Therefore, until more is known about the true phylogeny of the *Blepharida*-group genera worldwide, for the convenience of such catalogue arrangements, the author proposes that (based on the present morphological study) the following order of New World genera be used in catalogues and checklists:

*Blepharida* Chevrolat, 1837

(*Blepharida* Chevrolat *sensu stricto*)

(*Blepharidina* Bechyné, 1968)

(*Calotheca* Heyden, 1887)

(*Blepharidella* Weise, 1909)

*Notozona* Chevrolat, 1837

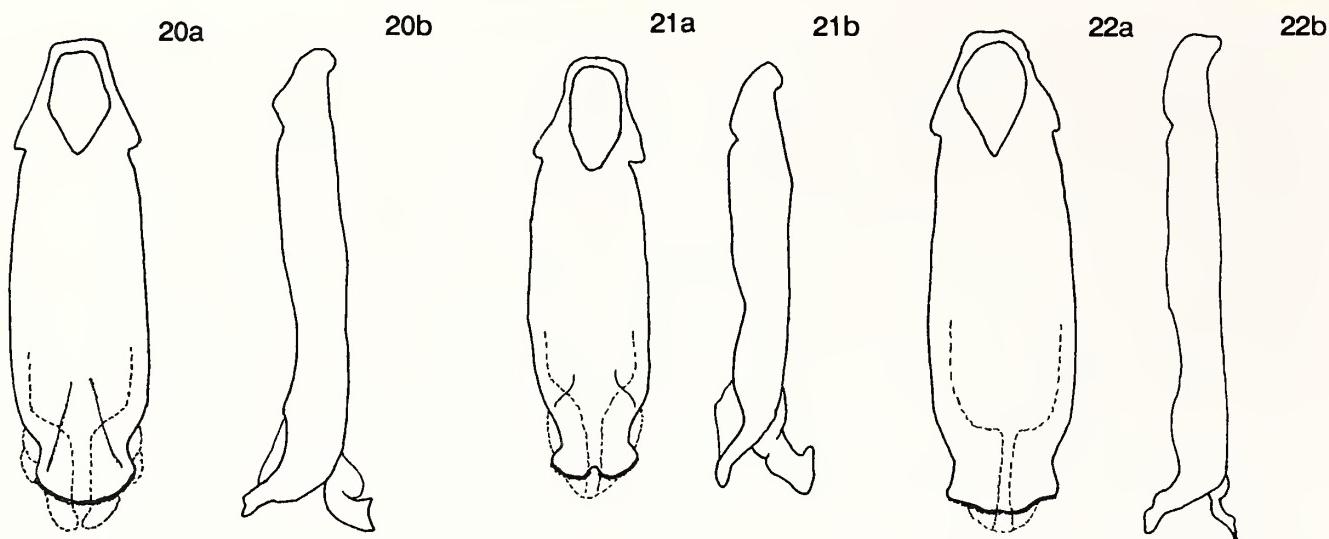
*Euplectroscelis* Crotch, 1873

*Blepharonycha* Fall, 1927

*Acrocyum* Jacoby, 1885

*Chrysogramma* Jacoby, 1885

Genera from the Afrotropical, Madagascan, and Pacific Ocean regions should be



Figs. 20–22. 20. *Blepharida franclemonti* aedeagus. a) ventral view b) lateral view ( $L = 3.40$  mm). 21. *Blepharida suturalis* aedeagus. a) ventral view b) lateral view ( $L = 3.22$  mm). 22. *Blepharida mexicana* aedeagus. a) ventral view b) lateral view ( $L = 3.52$  mm).

listed geographically after these New World genera, primarily for convenience, until their relationships to the other genera can be studied.

*Elithia* Chapuis, *Procalus* Clark, and *Crimissa* Stal should probably be left together as in the Seeno and Wilcox, 1982 checklist. Their relationship to the *Blepharida*-group genera is not apparent from the present study of external and internal morphology.

*Pseudorthygia* Csiki and *Phydanis* Horn are not related to the *Blepharida*-group and should not be included with them. Currently it is not clear where they should be placed in catalogues.

#### ***Blepharida franclemonti*, new species**

Figs. 4, 19, 20, 23

**Antennae.** color all yellow; average segment (1–11) lengths in millimeters 0.67, 0.23, 0.56, 0.59, 0.74, 0.56, 0.56, 0.52, 0.48, 0.44, 0.56.

**Head.** color yellow/light brown; clypeus smooth and impunctate; upper clypeus (lower frons) with deep transverse furrow, creating a prominent carina below (slightly wider in center); upper frons between antennal sockets with faint longitudinal carina, not raised, flattened with a few fine punctures, and only faintly delimited laterally by impressions; frontal bossae round, but poorly delimited, not raised and bordered only mesally and dorso-laterally by small depressions; a few very fine punctures along mesal eye margins; vertex with finely shagreened surface and very fine, sparse, confused punctures; eyes elliptical converging dorso-mesally (Fig. 4); average dorso-ventral eye length = 1.11 mm, average interocular distance (at dorso-mesal margins) = 1.04 mm.

**Pronotum.** color yellow/light brown; rectangular; lateral margins evenly, gradually rounded, slightly narrower at antero-lateral angles; antero-lateral angles obtuse, protruding laterally somewhat; punctuation very fine, with a few sparse, coarser punctures antero-lateral to midline; surface smooth with slight evidence of shagrination;



23a



24a



23b

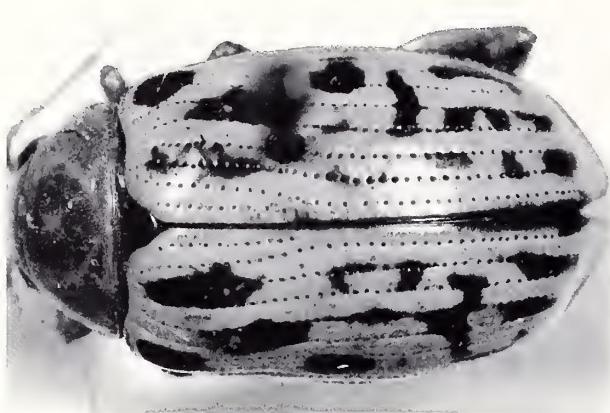


24b

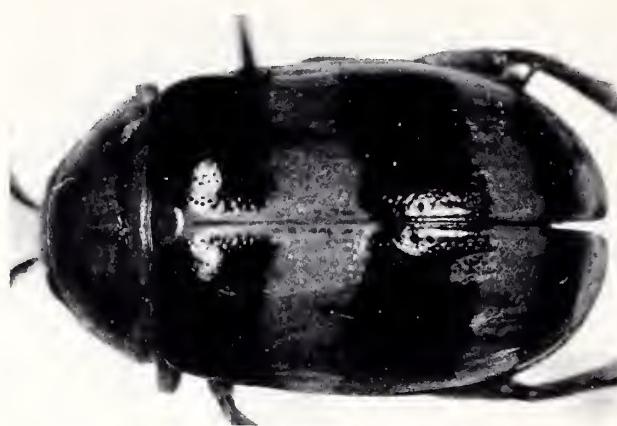
Figs. 23–24. 23. *Blepharida franclemonti* elytral pattern a) dorsal view b) lateral view (Length of elytra = Le = 6.80 mm). 24. *Blepharida suturalis* elytral pattern a) dorsal view b) lateral view (Le = 7.04 mm).

laterally often with small, gently depressed areas; average width at middle = 3.52 mm; average length at middle = 1.92 mm.

*Elytra.* striate with deep, medium-sized punctures; interstriae surface finely shagreened; background color chestnut/mahogany brown, with yellow markings; yellow pattern (Fig. 20a, b) often slightly assymetrical (fine details only); yellow pattern consisting mostly of yellow spots, sometimes contiguous, always on interstriae and distributed longitudinally, not forming transverse bands; third interstriae (between full puncture rows number 2 and 3 from suture, not including incomplete basal scutellar row) often with few or no spots; occasionally also small yellow spots near suture in middle or posteriorly; base of elytra with continuous, transverse yellow band (posterior borders irregular) surrounding the brown scutellum and continuous as a thin yellow longitudinal stripe along the base of the suture for approximately one quarter of elytral length; humeral callus prominent and surrounded by yellow (interstriae 6–9 with fused yellow spots surrounding brown humeral spot); fused yellow spots forming partial longitudinal stripes on interstriae 6 and 10 (lateral-most stria); spots on interstriae 6–10 often laterally forming small transverse bands of up to three interstriae wide; apically interstriae tapered and narrow, yellow spots often fused to form partial apical yellow band joining four or more interstriae; male elytral



25a



26a



25b



26b

Figs. 25–26. 25. *Blepharida mexicana* elytral pattern a) dorsal view b) lateral view (Le = 7.52 mm). 26. *Notozona bifasciata* elytral pattern a) dorsal view b) lateral view (Le = 6.24 mm).

length = 6.72–6.96 mm, width (at middle) = 5.04–5.20 mm; female elytral length = 7.04–7.68 mm, width = 5.28–5.60 mm; general body form similar to Chrysomelinae.

*Venter.* color yellow/light brown; pubescent throughout; procoxal cavities narrowly closed; prosternal process flat, apically expanded; mesosternal process with posterior margin emarginate; mesosternum vertically oriented; male apical sternite sublaterally cleft forming median, U-shaped lobe; apical tergite U-shaped; all sternites finely, densely punctate.

*Legs.* male first fore and midtarsal segments greatly expanded; metafemora elongate-oval in shape; metatibial dorsal edges, apically strongly emarginate, each edge with preapical protuberance; tarsal claws strongly bifid.

*Aedeagus.* in ventral view (Fig. 20a) apex evenly rounded with very rugose margin, subapical ventral surface with triangular raised area, tapered basally (also evident in lateral view); in lateral view (Fig. 20b) apex almost at right angle (dorsum/venter), extreme apex with small step-like angle, dorsal apical projection broadly hook-like; in dorsal view surface flat, dorsal projection with centrally tapering, subparallel, sclerotized ribs expanding apically into a short, umbel-shaped, sclerotized structure.

*Spermatheca.* Figure 19; slightly twisted ductus, visible only from ductus (right) side.



27a



28a



27b



28b

Figs. 27–28. 27. *Notozona histrionica* elytral pattern a) dorsal view b) lateral view (Le = 7.20 mm). 28. *Notozona nicaraguensis* elytral pattern a) dorsal view b) lateral view (Le = 8.56 mm).

**Differences from related species.** *B. franclemonti* is closest to *B. suturalis* Jacoby, 1885 (page 385, plate 22, fig. 12) and quite similar to *B. mexicana* Jacoby, 1885 (page 386, plate 22, fig. 16) differing from these primarily in elytral pattern and aedeagus morphology. *B. suturalis* differs from the new species by having the following characteristics: **Elytra** (Fig. 24a, b): more elytral yellow pattern, especially often forming transverse bands at apex and just in front of the middle; the yellow pattern usually as longitudinal stripes, not spots, especially along the apical two thirds of the second interstriae; first (sutural) interstriae without any yellow markings on apical two thirds, thus forming an apical brown sutural stripe; subbasal large brown areas; humeral and posthumeral brown spots; apex almost always with fused yellow, submarginal stripes. **Aedeagus:** Ventrally (Fig. 21a) deeply emarginate apex with less rugose margin; more prominently raised area subapically, diverging before tapering basally. Laterally (Fig. 21b) apical part (dorsum to venter) obtusely angled; extreme apex without step-like angle; dorsal apical projection broadly hook-like in shape; subapical raised area prominent. Dorsally surface deeply concave; dorsal projection with subparallel, more broadly tapered, median, sclerotized ribs, expanding apically into broad, umbel-shaped, more sclerotized apex than in *franclemonti* (more bullet-shaped apex). **Distribution:** Guatemala; El Salvador; Nicaragua; and Costa Rica.

*B. mexicana* differs from *B. franclemonti* as follows: **Elytra:** pattern (Fig. 25a, b), especially by having mostly yellow pattern with only a humeral brown spot and a few brown longitudinal, partial stripes, most notably on interstriae 3 and 5; most of sutural and subsutural interstriae yellow; apex entirely yellow. **Pronotum:** more quadrate (relatively longer than wide) than in the other two species. **Aedeagus:** ventrally (Fig. 22a) has a less rugose, more sinuate apical margin; laterally (Fig. 22b) no subapical raised area; dorsal projection (only slightly hook-shaped) pointing straight out apically; dorsally flat surface, dorsal projection with narrow, subparallel ribs, diverging apically, expanding laterally into lightly sclerotized, subumbel-shape (almost T-shape) with lateral angles acutely pointed. **Distribution:** Mexico (Oaxaca and Vera Cruz States).

**Etymology.** This new species is named for Prof. Emer. John G. Franclemont (Cornell University) who offered me valuable guidance and encouragement during my first few instars as a coleopterist, including during my first research on the genus *Blepharida*.

**Material examined.** HOLOTYPE: male, (MCZ type number 33406), Mexico, label data: "Mex: Yucatan, Chichen Itza 18–19 V 1987 D. A. Rider, E. G. & T. J. Riley." Deposited in the Department of Entomology, Museum of Comparative Zoology (MCZ), Harvard University as a donation from Edward G. Riley (EGR). ALLOTYPE: female (MCZ type number 33406), "Mexico, Yuc. Merida VII 29-30 1964 Paul J. Spangler." Deposited in the Department of Entomology, Museum of Comparative Zoology (MCZ), Harvard University as a donation from the National Museum of Natural History, Washington, D.C.—(USNM). PARATYPES: male (EGR), female (J. E. Wappes), "Mex., Quin. Roo 18–24 km N. San Felipe Carr. pte. 5/27/–6/1/84, J. E. Wappes"; 3 males (1 EGR, 2 Robert Turnbow-RT), female (RT), "Mex, Quintana Roo, 18 km N. Carrillo Puerto, at lite. 31 May 1984 R. Turnbow"; 3 females (USNM), same data as Allotype; female (American Museum of Natural History, New York—AMNH), "Piste. Yucatan Mex. VI 8–10 59 P. & C Vaurie"; female (AMNH), "Mex., Yucatan Piste June 3–5, 59 P. & C. Vaurie"; female (The Natural History Museum, London), "55 24," "Jac," "Baly Coll"; female (MCZ), "Mex"; female (MCZ), "Yucatan."

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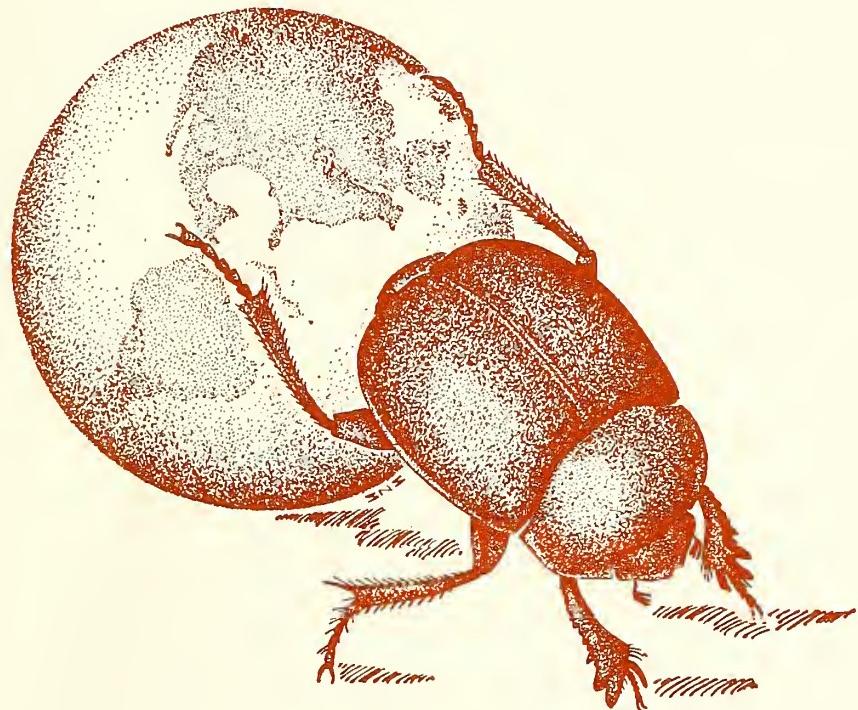
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## NEW SYNONYMS OF *FRANKLINIELLA BONDARI* AND A REVIEW OF THE SYNONYMS OF *F. CEPHALICA* (THYSANOPTERA: THRIPIDAE)

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*Abstract.*—*Frankliniella alba* Moulton and *F. bratleyi* Watson are junior synonyms of *F. bondari* Hood (New Synonymy). The seven species and varieties of *Frankliniella* treated as junior synonyms of *F. cephalica* (Crawford) in the “Catalogue of the Thysanoptera of the World” (1974), are not synonyms. *Frankliniella bispinosa* (Morgan), *F. bruneri* Watson, *F. echinodora* Moulton, *F. melanommata* Williams and *F. reticulata* (Crawford) are treated as valid species. *Euthrips tritici* var. *projectus* Watson and *Frankliniella cephalica* var. *masoni* Watson are junior synonyms of *F. bispinosa* (New Synonymy).

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*Frankliniella bondari* Hood (1942:622) and *F. bratleyi* Watson (1942:17) described from tuberose, *Polianthes tuberosa* L. (Agavaceae), are synonyms based on my examination of the types. The types of *F. bondari* were collected in Bahia, Brazil, and consist of only macropterous females. The types of *F. bratleyi* were collected in Gainesville, Florida, on damaged bulbs and consist of macropterous and brachypterous females. Hood’s paper was published in January, 1942 and Watson’s paper in June, 1942. Thus, *F. bondari* has priority and *F. bratleyi* is treated here as the junior synonym (New Synonymy).

*Frankliniella alba* Moulton (1948:113) was described from two females (macropterous and brachypterous) found on gladiolus from Mexico. The macropterous holotype examined in this study is similar to *F. bondari* except for its longer posteroangular setae on the pronotum. The lengths of these setae vary in material of *F. bondari* examined, and I conclude that *F. alba* is another junior synonym of *F. bondari* (New Synonymy). The holotype of *F. alba* is deposited in the Thysanoptera collection of the U.S. National Museum of Natural History, not in the California Academy of Sciences as indicated by Jacot-Guillarmod (1974:762).

*Frankliniella bondari* has pale yellow body, wings and setae, and the head is slightly produced anterior of the eyes. In this country, it resembles *F. unicolor* Morgan. *Frankliniella bondari* has the basal one-third to one-half of antennal segment VI yellow and the interocellar setae are positioned between the anterior and posterior ocelli, whereas *F. unicolor* has completely brown antennal segment VI and the interocellar setae are positioned laterad of the anterior ocellus.

The known distribution of *F. bondari* is Brazil, Mexico, and the United States (Florida, Georgia and Hawaii). I have also examined a quarantine interception from Israel and another from Cuba on *Polianthes* sp.

The preferred host is *Polianthes tuberosa* and some of the other recorded hosts probably are incidental. According to “Hortus Third,” the species of *Polianthes* originated in Mexico. The thrips apparently also originated in Mexico and was introduced into other countries on the rhizomes of tuberose, which is grown com-

mercially and in gardens for the waxy-white, fragrant flowers. This species was recently discovered in the state of Hawaii on the islands of Molokai and Oahu where it damages tuberose.

Jacot-Guillarmod (1974:767) treated the following seven taxa as junior synonyms of *Frankliniella cephalica* (Crawford) (1910:153) in his "Catalogue of the Thysanoptera of the World."

*Euthrips cephalicus* var. *reticulata* Crawford, 1910:153.

*Euthrips tritici* var. *bispinosus* Morgan, 1913:10.

*Frankliniella melanommatus* Williams, 1913:213.

*Euthrips tritici* var. *projectus* Watson, 1915:51.

*Frankliniella cephalica* var. *masoni* Watson, 1919:4.

*Frankliniella cephalica* var. *bruneri* Watson, 1926:54.

*Frankliniella cephalica* var. *echinodora* Moulton, 1948:107.

In this review of the synonyms, I conclude that none of these taxa are junior synonyms of *F. cephalica*.

The lectotype of *E. cephalicus* var. *reticulata*, which is deposited in the Canadian National Collection, was examined. On the type slide are also seven yellow specimens, of which five are *F. borinquen* Hood and two are *F. cephalica*. In my opinion, *reticulata* is a distinct species in *Frankliniella* (New Status). The body is uniform brown as described by Crawford (1910:153). It also differs morphologically from *F. cephalica* in the shape of antennal segment II and enlargement of the pedicel of antennal segment III, and by having on abdominal tergite VIII, a complete postero-marginal comb which is medially incomplete in *F. cephalica*.

Sakimura (1981:484, 1986:354) treated *F. bruneri* and *F. melanommata* as good species.

Although a formal redesignation has not been published, *F. bispinosa* in recent years has been given species status in identifications, reports and publications (i.e., Beshear, 1979:210) for the following reasons: the pedicel of antennal segment III of *F. bispinosa* is larger and differently shaped than that of *F. cephalica*, and in Florida and Bermuda, *F. cephalica* is normally found in the flowers of *Bidens* sp. and *F. bispinosa* in various flowers. *Frankliniella bispinosa* is recorded from Florida, Georgia, South Carolina, Bahama Islands and Bermuda.

In my opinion, *F. cephalica* var. *masoni* and *E. tritici* var. *projectus* are junior synonyms of *F. bispinosa* (New Synonymy).

The holotype and allotype of *F. cephalica* var. *echinodora* differ from *F. cephalica* in the shapes of the enlargement of the pedicel and basal part of antennal segment III. For these reasons, I treat the two taxa as different species (New Status). *Frankliniella echinodora* is known only from Puerto Rico. Jacot-Guillarmod (1974:770) stated that the types were deposited in the California Academy of Sciences. The paratypes are deposited in that museum but the holotype and allotype are deposited in the Thysanoptera collection of the U.S. National Museum of Natural History.

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**THE FIRST RECORDS OF THE FAMILIES OCHTERIDAE AND  
HEBRIDAE (HETEROPTERA) FROM THE GRANITIC  
SEYCHELLES, WITH DESCRIPTIONS OF  
TWO NEW SPECIES**

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*Abstract.*—The families Ochteridae and Hebridae are recorded for the first time from the granitic Seychelles, based on collections from mountain streams on the island of Mahe. Two new species, *Ochterus seychellensis* and *Hebrus seychellensis*, are described, with dorsal habitus and male genitalic figures.

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The aquatic Heteroptera fauna of the granitic Seychelles is of interest from a biogeographical standpoint, since it is hypothesized that these oceanic granitic islands represent small continental fragments stranded in the wake of drifting India (Davies, 1968). Up to the present time the fauna has appeared to be relatively similar to that occurring on the high islands of the Mascarenes, consisting primarily of vagile, widespread species of common occurrence throughout the western Indian Ocean basin. Several recent discoveries, however, have revealed that the granitic Seychelles do in fact harbor a significantly richer fauna than the Mascarenes, including the unusual mesoveliid genus *Phrynovelia* (Andersen, in press) and two species of the genus *Rhagovelia* (J. Polhemus, 1990). To these discoveries may now be added two new species belonging to the families Ochteridae and Hebridae, which were previously unknown from any of the high Indian Ocean islands between Madagascar and Ceylon. The relationships of these new species have yet to be resolved, since the genera *Ochterus* and *Hebrus* to which they belong are both large and in need of revision in the Eastern Hemisphere, but their presence indicates that the granitic Seychelles may indeed harbor the remnants of an old continental aquatic Heteroptera fauna that was fragmented by vicariance events during the breakup of the Gondwana supercontinent.

The collections on which the new taxa in this paper are based were made by the author during his participation in the Smithsonian Institution's Aldabra Program and were undertaken in cooperation with the Seychelles Islands Foundation. The holotypes are deposited in the collections of the National Museum of Natural History, Washington, D.C. (USNM); paratypes are also deposited in the J. T. Polhemus collection, Englewood, Colorado (JTPC). All measurements are given in millimeters. The CL numbers following locality data refer to codes used by the author to reference ecological notes.

***Ochterus seychellensis*, new species**

*Diagnosis.* This species may be separated from any other *Ochterus* presently described from India, Ceylon, Africa or Madagascar by the following combination of characters: the rostrum exceeds the hind coxae; the clavus and corium are smooth,

without deep punctations; the hemelytra lack gold scale-like setae; and the embolium is only weakly punctate. The absence of punctations on the distal part of the inner corium is a character state not seen in any other Old World species.

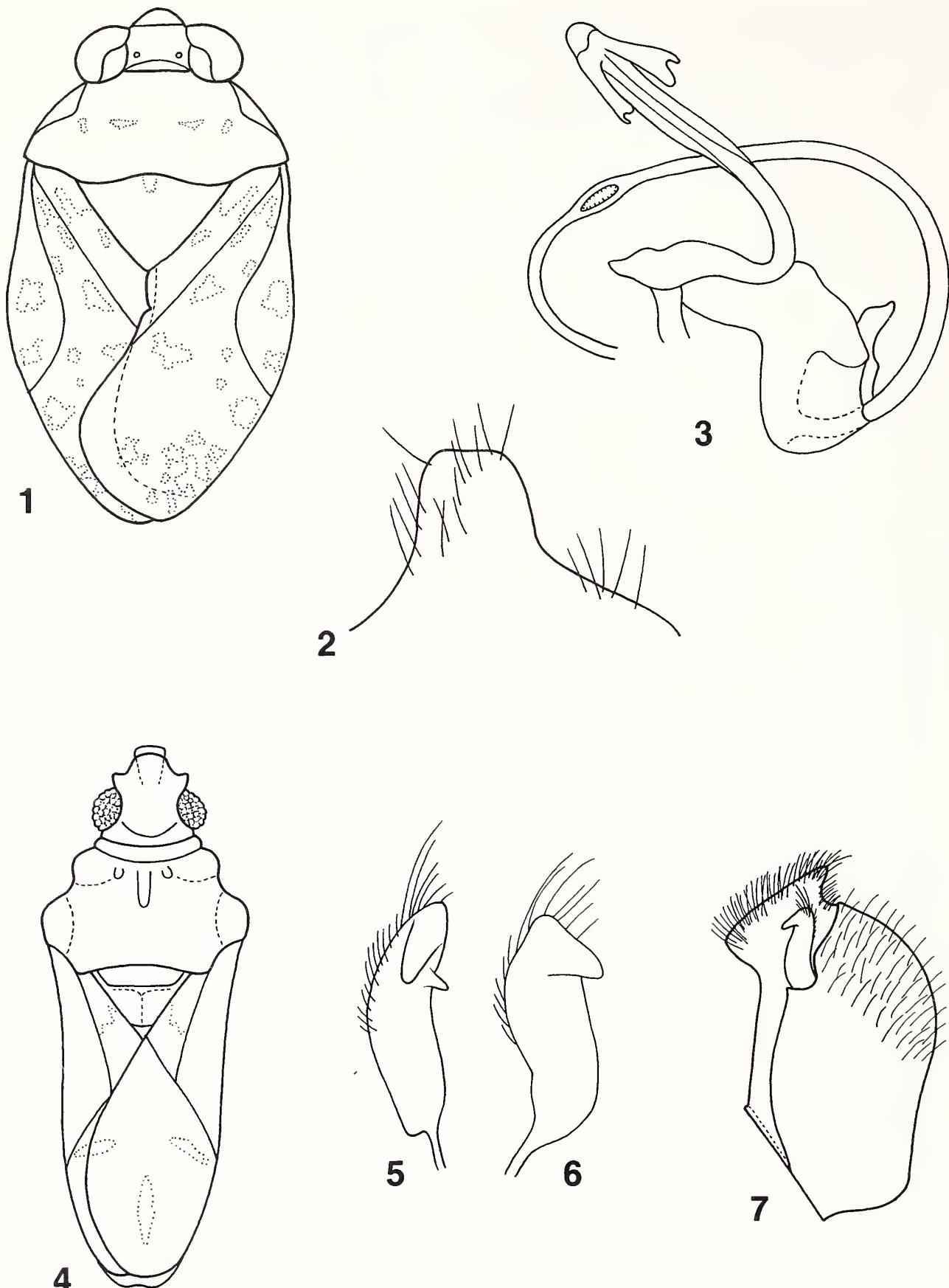
*Description.* Male: general form broadly ovate, body length 4.31 mm; maximum width 2.42 mm (Fig. 1). General coloration dark velvety green, with scattered pruinose lavender markings as follows: narrow linear patches at base of ocular flanges and along anterior pronotal margin adjoining vertex; four small irregular patches arranged transversely between anterior and posterior lobes of pronotum; single small triangular patch medially along anterior margin of scutellum; broad irregular patches basally on each half of clavus and corium; two large roughly circular patches on each embolium; 5 to 6 irregular patches of varying size on each half of central corium; irregular network of partially interconnected patches on wing membrane. Head shining black; anterior margin of clypeus, anterolateral and posterior margins of pronotum, anterolateral margin of embolium, rostrum, legs and abdominal venter dark yellow; antennal segments I and II pale yellow, segments III and IV pale brown; thoracic venter dull pruinose black; hind tibiae spotted with black at bases of stout erect spines.

Head glabrous, length (along midline as measured from directly above)/width (across eyes) = 0.39/1.34, angled downward at 45° when viewed laterally; vertex with numerous striae; eyes large, protruding, projecting posteriorly behind vertex; antennae with segments I and II short, globose, segments III and IV slender, filiform, lengths of segments I–IV = 0.11, 0.11, 0.28, 0.31; rostrum long, length = 2.58, exceeding hind coxae and extending onto base of abdominal venter.

Pronotum length (midline)/width = 1.06/2.21, bearing numerous small glabrous punctations, lacking evident setae; anterior collar prominent, flat; anterolateral margins explanate, well demarcated from disk; calli weakly tumescent; posterior margin multisinuate, posteriorly concave centrally above base of scutellum. Scutellum triangular, length/width = 0.73/1.34, weakly tumescent, bearing numerous small glabrous punctations centrally plus a double row of slightly larger, more closely spaced punctations along lateral margins, lacking evident setae. Hemelytra long, attaining tip of abdomen, corium, clavus and embolium well defined, surfaces smooth, sparsely set with very tiny gold setae, lacking evident punctations except for a few very tiny punctations on embolium; anterolateral embolar margin explanate; length of clavus along outside margin = 1.79; membrane venation evident, defining 7 closed cells.

Ventral surface of thorax smooth and pruinose, lacking setae, bearing scattered punctations on pro-, meso-, and metaepisterna; abdominal venter covered with very short fine appressed gold setae, this setal covering interrupted by ovate glabrous patches surrounding spiracles laterally on paratergites. Leg segments covered with short, fine, recumbent gold setae; anterior and middle tibiae bearing numerous short bristly gold setae, these setae becoming more numerous distally; fore and middle tibiae with a few longer semi-erect spinelike setae on posterior margins; hind tibia with double longitudinal row of large erect gold spines; all tibiae with transverse rows of spines at distal ends; claws gold, gently curving, arolia long, exceeding length of claws when viewed laterally.

Genital segment well retracted into abdomen; subgenital plate with V-shaped indentation medially on posterior margin. Pygophore quadrate, apex transverse, lateral lobes well removed from apex (Fig. 2). Right paramere with head of moderate height,



Figs. 1–3. *Ochtherus seychellensis*, n. sp. 1. Male, dorsal habitus (legs omitted). Locations of pruinose lavender patches defined by stippling. 2. Male pygophore, caudal tip. 3. Male genital complex.

Figs. 4–7. *Hebrus seychellensis*, n. sp. 4. Male, dorsal habitus (legs omitted). Locations of white markings on hemelytra defined by stippling. 5. Male right paramere, top view. 6. Male right paramere, lateral view. 7. Male genital capsule, left lateral view.

evenly domed and convex; appendices moderately long, apices indented; shaft stout, broadened distally (Fig. 3).

Female: Similar to male in general structure and coloration but slightly smaller, body length 4.06, width 2.35.

*Discussion.* *O. seychellensis* n. sp. is immediately separable from the widespread *O. marginatus* occurring on India and Ceylon, which possesses numerous punctations on the clavus and corium, and alternating brown and yellow spots on the margins of the hemelytra, and from the somewhat similar *O. minor* from Africa, which also has punctate hemelytra and dark yellow spots along the wing margins, a yellowish area centrally on the posterior margin of the pronotum, and a shorter rostrum that does not exceed the hind coxae. *O. seychellensis* n. sp. is also separable from the south and east African *O. caffer*, which is much larger, has punctate hemelytra and a short rostrum which does not exceed the hind coxae, and lacks the bluish pruinosity at the base of the clavus.

The general habitus and smooth hemelytra of *O. seychellensis* n. sp. are reminiscent of a group of Neotropical ochterids which also occur on vertical rock faces, but these resemblances appear to be due to convergence rather than monophyly, since the New World species have a very different male genitalic plan.

*Etymology.* The name "seychellensis" refers to the Seychelles islands.

*Habitat data.* The type series was taken from a wet vertical rock wall along the Foret Noire road near the Congo Rouge trailhead; this is close to the highest point that can be reached by road on the island of Mahe. The rock face was formed by the road cut, with disturbed secondary rain forest immediately above it. A shallow flow of water trickled down across the face, collecting in a narrow concrete channel at its base. The face itself was irregular and covered with alternating patches of moss and open wet rock, and the ochterids moved across it with great agility, being quick to fly if pursued or otherwise disturbed. To slow their movements a small amount of pyrethrin insecticide was sprayed on the rock face; this application resulted in the appearance of many previously undetected ochterids which had apparently been secreted amid the moss or in cracks in the rock. This treatment also resulted in the appearance of an undescribed species of *Phrynovelia* (Andersen, in press) which appears to share the rock face habitat with *O. seychellensis*. Another single specimen of *O. seychellensis* was taken along the upper Riviere Grande Bois on the opposite side of the road from the rock face, and several other individuals were seen along this stream. All were on shaded mossy rock walls and overhangs near the water, and were once again very fast and difficult to catch.

On the basis of these observations *O. seychellensis* seems to be confined to vertical wet rock faces, a preference quite distinct from that of many other Old World ochterids which more typically occupy sandy horizontal substrates adjacent to streams and ponds. It seems likely that this species is probably more widespread on Mahe than the present records indicate, but that its obscure habitat and difficulty of capture have precluded its collection.

*Holotype.* Male: SEYCHELLES, Mahe, seeping rock faces along Foret Noire road near Congo Rouge trailhead, 390 m, 3 April 1989, CL 8047, D. A. Polhemus (USNM).

*Paratypes.* SEYCHELLES, Mahe: 15 ♂♂, 22 ♀♀, same data as holotype (USNM, JTPC); 1 ♂, headwaters of Riviere Grande Bois, along Foret Noire road near Congo Rouge trailhead, 420 m, water temp. 22.5°C., 3 March 1989, CL 8016, D. A. Pol-

hemus (USNM); 1 ♂, Riviere Grand Bois, 6.2.74, F/Sey/4., F. Starmühlner (JTPC).

*Additional specimens not paratypes.* SEYCHELLES, Mahe: 18 immatures (stored in alcohol), same data as holotype (USNM).

### ***Hebrus seychellensis*, new species**

*Diagnosis.* This species may be separated from other *Hebrus* presently known in Africa, Madagascar and India by the following characters: the large keeled triangular male proctiger thickly set with erect curving setae (Fig. 7); the distinctive male paramere shape with a spur on the inner face (Figs. 5, 6); the bowed hind femur; the unmodified hind tibia; the shape of the posterior margin of the bucculae; the setose areas distally on the anterior and middle tibiae; the tumescent abdominal ventrite VI in females; and the pattern of white markings on the hemelytra (Fig. 4).

*Description.* Macropterous male: elongate, body length/width (across humeri) = 2.02/0.77. Ground color dark brown; eyes reddish brown; rostrum dark yellow; lateral portions of anterior lobe of pronotum dark brown; hemelytra dark blackish brown with white patches basally on clavus to either side of scutellum, membrane fumate, with 3 elongate white streaks posteriorly (Fig. 4); legs dark yellow brown, becoming more infuscated on distal portions of femora and tibiae; venter of thorax medium brown, venter of abdomen black.

Head long, declivant anteriorly, length (as measured from directly above)/width (across eyes) = 0.40/0.43, width across antennal tubercles = 0.32; vertex lacking a median sulcus. Eyes moderately large, exserted, globose, coarsely faceted; ocellar pit located mesad of posterior portion of eye; ocelli of moderate size, evident, eye width/interocular space = 0.09/0.24. Antennae long, slender, lengths of segments I–IV = 0.29, 0.20, 0.45, 0.27; segments I and II stoutest, of similar diameter, bearing short pale recumbent setae, segments III and IV more slender, bearing longer erect pale setae whose lengths exceed the segment diameters. Rostrum long, length = 0.88, extending past hind coxae and onto base of abdomen. Bucculae long, prominent, bearing 5 foveae, with 2 large foveae along dorsal margin adjoining gula and 3 smaller foveae evenly spaced around the posterior buccular margin.

Pronotum long, length/width (across humeri) = 0.50/0.79, weakly constricted medially, bearing median longitudinal sulcus. Anterior lobe with 2 (1+1) deep pits to either side of longitudinal midline, anterior margin with prominent collar. Posterior lobe tumid, raised above anterior lobe, lacking significant pits or depressions posteriorly, humeri prominent. Scutellum length/width = 0.22/0.41; mesoscutellum short, raised, length 0.05; metanotum moderately long, length/width = 0.16/0.29, with weak longitudinal median carina, posterior margin raised to form a horizontal lip.

Hemelytra complete, attaining tip of abdomen; costal margin and corium thickened, set with numerous fine recumbent gold setae.

Legs moderately stout, straight, all segments covered with short semi-recumbent gold setae, fore and middle tibiae with thicker patches of setae distally on ventral faces; proportions of leg segments as follows: fore femur/tibia/tarsal 1/tarsal 2 = 1.10, 1.06, 0.80, 0.31; middle femur/tibia/tarsal 1/tarsal 2 = 1.06, 1.02, 0.08, 0.27; hind femur/tibia/tarsal 1/tarsal 2 = 1.33, 1.57, 0.08, 0.47.

Venter of thorax weakly pruinose, sparsely set with short gold setae; abdominal venter shining, more thickly covered with short recumbent gold setae, central portion

of ventrite VI glabrous and broadly but distinctly tumescent, this tumescence most evident when viewed laterally.

Genital segment of moderate size, mostly retracted into abdomen; proctiger triangular, bearing an anteromedial keel-like structure thickly set with erect curving setae (Fig. 7); parameres symmetrical, hooked at tips with spur on inner face, shape as in Figures 5, 6.

Macropterous female: similar to macropterous male in general structure and coloration but slightly larger. Body length 2.15 mm, width (across humeri) 0.86 mm.

*Discussion.* The genus *Hebrus* is in serious need of revision in the Old World, and the number of species in Africa, Madagascar and tropical Asia is so large that individual comparisons with *H. seychellensis* n. sp. would be impractical. The characters given in the diagnosis and the geographical provenance should, however, be sufficient to allow easy recognition of this species.

*Etymology.* The name "seychellensis" refers to the Seychelles islands.

*Habitat data.* The type series was taken along the Riviere Grande Saint Louis above the Le Niol water intake, a clear rocky stream coming down out of a disturbed primary rain forest catchment. The insects were very uncommon, and were found only on the dark undersides of large midstream rocks which projected out over the flowing water.

*Holotype.* Macropterous male: SEYCHELLES, Mahe, Riviere Grande St. Louis above Le Niol water intake, 330 m, water temp. 22.5°C., 2 April 1989, CL 8046, D. A. Polhemus (USNM).

*Paratypes.* 1 macropterous ♂, 1 macropterous ♀, same data as holotype (USNM, JTPC).

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**A REVIEW OF THE SPECIES OF ANTHOCORIDAE  
(HEMIPTERA: HETEROPTERA) FOUND ON  
*PINUS CONTORTA***

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*Abstract.*—The Anthocoridae fauna found on the widespread western North American pine, *Pinus contorta*, is reviewed. Ten genera and 18 species are reported. Three of these species (*Anthocoris* spp. and *Orius tristis*) are considered casual visitors to the tree. Biological, ecological, and taxonomic information is presented for each species and the pertinent literature reviewed.

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*Pinus contorta* Dougl., ex Loud, with four subspecies, is the most widespread species of pine in North America (Critchfield, 1957, 1980, 1985; Critchfield and Little, 1966; Wheeler, Guries, and O'Malley, 1983; McCune, 1988). Commonly known as lodgepole pine throughout much of its range, the northern coastal subspecies is referred to as shore pine and the unusual dwarf subspecies is called pygmy pine. Forrest (1980a, b) recognized a number of chemical regions for *Pinus contorta*, based upon studies on the variation found in foliar monoterpenes. The subspecies occur in northern Baja California, on the north coast of California, north through Oregon, Washington and British Columbia, in the Sierra Nevada and Cascade Mountains north to the Yukon Territory, and south through the Rocky Mountains and adjacent areas to southern Colorado (Critchfield, 1957). It grows from sea level in Oregon to 12,000 feet (3,900 m) in the southern Sierra Nevada mountains (Critchfield, 1980).

We have collected Hemiptera: Heteroptera from this tree species regularly at six sites in Oregon and Wyoming. Other collections have been made at various localities in different parts of the range of *P. contorta*, and to a lesser extent, on some of the other species of conifers occurring with *P. contorta*. The family Miridae is particularly well represented on this conifer (approximately 57 species known to date; unpublished data), and so it seems are the Anthocoridae. The diverse habits of the various species of anthocorids and their particular habitat requirements, often remarkably specific, combined with the enormous ecological and geographical range of *P. contorta* result in a diverse fauna of 10 genera and 18 species (24 genera and 90 species occur in America north of Mexico [Henry, 1988]).

The objective of this paper was to coalesce information on the systematics, habitats, plant hosts, prey species, and geographic distribution for those 18 species of North American Anthocoridae found on *Pinus contorta*. The primary source of information is based upon our regular sampling of three sites in Oregon on *P. contorta contorta*, *P. c. latifolia*, and *P. c. murrayana*, and three sites on *P. c. latifolia* in Wyoming. Additional records come from specimens examined in several collections and from

the literature. We have summarized the available literature on each species treated, including taxonomic, biological, and ecological information. Appropriate literature records are presented in the condensed bibliographic style of taxonomic papers for brevity.

#### SYSTEMATICS

The Anthocoridae comprise a small family of Hemiptera: Heteroptera with about 80 genera and 450 species world-wide (Péricart, 1972). Henry (1988) reported 23 genera and 89 species from America north of Mexico. An additional genus and species, *Brachysteles parvicornis* (Costa), has been reported recently from the East Coast where it was taken under the bark of pine trees and beaten from *Picea* and *Pinus* branches (Asquith and Lattin, 1990; Lattin and Asquith, 1991). Approximately one-third of the species north of Mexico occur on conifers. Others are found on broad-leaved plants or in leaf litter.

Péricart (1972) provided an extensive treatment of the Anthocoridae of western Europe and permitted the comparison of elements of our fauna with those of the European continent. Herring (1976) published a key to the genera of Anthocoridae north of Mexico. Anderson (1962b) provided the most detailed summary of the Anthocoridae of the Pacific Northwest. Kelton (1978) is the only modern, comprehensive treatment of the family for North America. Earlier, he published several generic revisions of the North American species (Kelton, 1963, 1966a, 1967, 1976b) as Herring (1966) did for *Orius*. Much additional biosystematic work remains to be done on the Anthocoridae.

The higher classification of the Heteroptera is undergoing substantial change, with increased emphasis on cladistic analysis (see Schuh, 1986, for an important review). The suborder Cimicomorpha, which contains the Anthocoridae, is being reviewed by several investigators. Major changes in classification of the Anthocoridae have been suggested by Schuh (1986; pers. comm., April, 1991), based on evidence given by Ford (M.S. thesis). Schuh and Stys (1991) provided a detailed account of some of these changes. We have taken a rather conservative approach in this paper with the recognition that future phylogenetic studies are certain to modify the current definition of the family. Such information will aid in interpreting biological and ecological data.

#### METHODS

We collected ten genera and 18 species on *P. contorta*. The genera and species reported here are arranged alphabetically for ease of reference. Table 1 shows the same taxa arranged by systematic scheme (Carayon, 1972a; Péricart, 1972; Henry, 1988).

*Collection sites:* We have collected regularly at three sites in Oregon and three sites in Wyoming from April to October in 1986. Rather than repeat these localities in full, we will describe them here and refer to them together with the dates of collection. Collections made at other times and places are described in full. Branches of conifers were firmly beaten with an axe handle and the dislodged anthocorids were collected from the beating sheet held under the branch.

Oregon: Site 5: Lincoln Co., 1.6 km S Newport, South Beach State Park, R11W,

Table 1. Species of Anthocoridae collected from *Pinus contorta* subspp. arranged by current classification. \* Indicates incidental occurrence.

Anthocoridae
Anthocorinae Reuter, 1884
Anthocorini Reuter, 1884
<i>Acompocoris lepidus</i> (Van Duzee)
* <i>Anthocoris antevolens</i> White
* <i>Anthocoris musculus</i> (Say)
<i>Elatophilus dimidiatus</i> (Van Duzee)
<i>Elatophilus pullus</i> Kelton and Anderson
<i>Elatophilus</i> sp. A
<i>Melanocoris longirostris</i> Kelton
<i>Melanocoris nigricornis</i> Van Duzee
<i>Tetraphleps canadensis</i> Provancher
<i>Tetraphleps latipennis</i> Van Duzee
<i>Tetraphleps pilosipes</i> Kelton and Anderson
<i>Tetraphleps uniformis</i> Parshley
Oriini Carayon, 1955
* <i>Orius tristicolor</i> (White)
Lyctocorinae Reuter, 1884
Dufouriellini Van Duzee, 1916
<i>Cardiastethus borealis</i> Kelton
Lyctocorini Reuter, 1884
<i>Lyctocoris tuberosus</i> Kelton and Anderson
Scolopini Carayon, 1954
<i>Scoloposcelis flavigornis</i> Reuter
Xylocorini Carayon, 1972
<i>Xylocoris californicus</i> (Reuter)
<i>Xylocoris cursitans</i> (Fallén)

T11S, SW $\frac{1}{4}$  Sec. 20. ex *Pinus contorta contorta* Dougl. ex Loud. Site 7: Crook Co., 40 km E Prineville, 1,476 m elev., R19E, T13S, SW $\frac{1}{4}$  Sec. 2. ex *Pinus contorta latifolia* Engelm. Site 8: Deschutes Co., Three Creeks Meadow, 2,069 m, 26 km S Sisters, R9E, T17S, SW $\frac{1}{4}$  Sec. 13 ex *Pinus contorta murrayana* (Grev. & Balf.) Engelm.

Wyoming: Site 2: Albany Co., Medicine Bow Nat. For., Happy Jack Road, 19 km E Laramie, 2,500 m, R72W, T15N Sec. 25. ex. *Pinus contorta latifolia*. Site 3: Albany Co., Snowy Range Mountains, North Fork Camp ground, Sand Lake Road, 2,800 m, 60 km W. Laramie, R78W, T16N, Sec. 17, ex *Pinus contorta latifolia*. Site 4: Carbon Co., Snowy Range Mountains, French Creek Road, 2,750 m, 90 km W. Laramie, R81W, T15N, Sec. 1 & 17. ex. *Pinus contorta latifolia*.

*Collections examined:* All specimens are housed in the Systematic Entomology Laboratory (OSU-SEL), Department of Entomology, Oregon State University, unless otherwise indicated. Additional material was examined from the Canadian National Collection, Ottawa, Canada (CNC), Oregon Department of Agriculture (ODA), Salem, and from the U.S. Forest Service, Pacific Northwest Research Station, LaGrande, Oregon, collection (USFS-LaGrande). Supportive material was examined from the

California Academy of Sciences, San Francisco, the University of California, Riverside, and the United States National Museum, Washington, D.C.

The section that follows presents information about each species of Anthocoridae found on or reported from *Pinus contorta*. A bibliography is given for each species to provide access to the biological and systematic literature. Diagnostic characters are included to assist in recognition. Information on habitat and host plant association, prey, life history, and distribution is reviewed and summarized followed by documentation of specimens collected and examined during this study.

#### BIONOMICS

##### *Acompocoris* Reuter

*Acompocoris* Reuter, 1875:63; Harris and Shull, 1944:207; Péricart, 1972:146; Herring, 1976:146; Kelton, 1978:32; Henry, 1988:13.

**Diagnosis:** Normally macropterous (membrane of female may be slightly reduced); shiny, usually pubescent; rostrum almost reaching or exceeding hind coxae; hind coxae proximate; ostiolar canal broad, slightly curved in anterior direction, apex extended anteriorly as fine carina (Péricart, 1972; Kelton, 1978). North American species with head, pronotum, and scutellum, dark brown to black in contrast to pale brown hemelytra.

*Acompocoris* Reuter contains six species in the Holarctic Region (Péricart, 1972). Species of the genus are found only on conifers where they appear to feed on aphids, especially members of the genus *Cinara* Curtis. Two occur in North America, *A. lepidus* (Van Duzee) from California and the introduced European species, *A. pygmaeus* (Fallén). Host plant genera for North American *Acompocoris* include *Pinus* (most common), *Picea*, *Larix*, and *Abies* (Péricart, 1972; Kelton, 1978). Only *A. lepidus* occurs on *P. c. murrayana*. *Acompocoris pygmaeus* was reported from *P. sylvestris* in Nova Scotia and New Brunswick (Kelton 1977a) and *P. strobus* (Kelton, 1978).

##### *Acompocoris lepidus* (Van Duzee) (Figure 1)

*Tetraphleps lepidus* Van Duzee, 1921:142.

*Acompocoris lepidus*: Kelton and Anderson, 1962:1307; Mitchell, 1962:53; Anderson, 1962b:1332; Kelton, 1977a:245; Kelton, 1978:32; Henry, 1988:13.

*Acompocoris* sp. Harris and Shull, 1944:207.

**Diagnosis:** Macropterous species about 3.5 mm long; shiny with long pubescence; apex of rostrum attaining or surpassing hind coxae. Color dark brown to black, pronotum entirely black, hemelytra brown, shiny; antennal segment 2 dark, pale at middle. Resembles species of *Tetraphleps* but apex of ostiolar canal not elevated above metapleuron, continued forward as fine carina (apex of canal elevated above metapleuron in *Tetraphleps*).

**Habitat:** Little specific information is available on the preferred habitat of this species, which was originally described from specimens collected on *Pinus contorta murrayana* in California (Van Duzee, 1921); and later reported from *P. ponderosa*

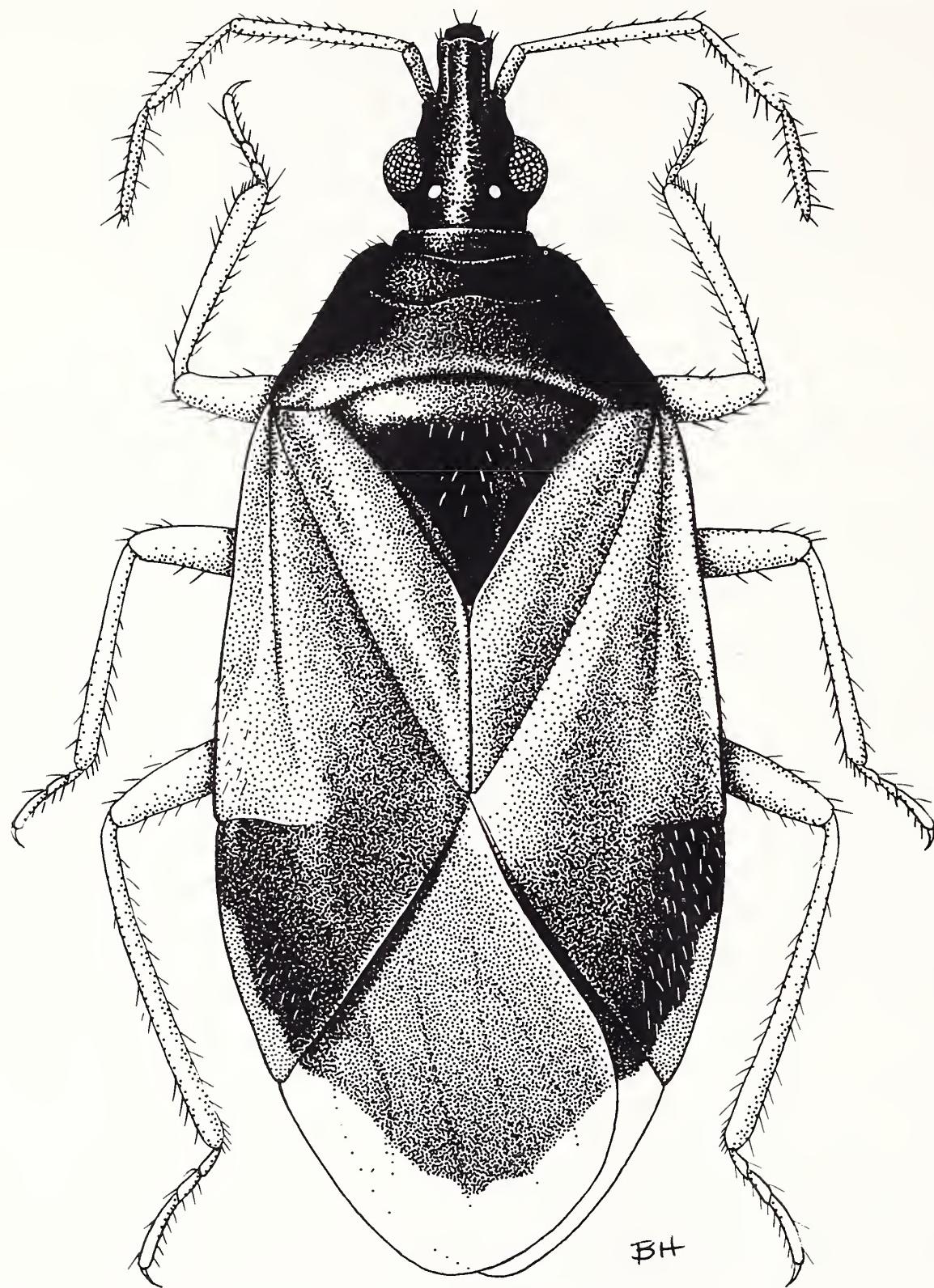


Fig. 1. *Acomporis lepidus* (Van Duzee).

and *Picea engelmanni* in British Columbia (Kelton, 1978). We report it here from *P. c. murrayana* in the central Oregon Cascade Mountains and on *P. c. latifolis* in British Columbia, the Yukon Territory, and in Wyoming.

**Prey:** Mitchell (1962) considered *A. lepidus* an effective predator of the balsam woolly aphid.

**Phenology and life history:** Type specimens were collected in late July in southern California. Adults were collected in July in Wyoming, August in British Columbia,

Oregon, Wyoming, and Yukon Territory, and September in Colorado, Oregon, and Wyoming. No information is available on the life history of this species.

**Distribution:** *Acompocoris lepidus* was described from Huntington Lake, 2,277 m, Fresno Co., California (as a species of *Tetraphleps*). Harris and Shull (1944) reported an unidentified species of *Acompocoris* from McCall, Idaho (presumably *A. lepidus*). Mitchell (1962) reported *A. lepidus* from the central Cascade Mountains of Oregon. Anderson (1962b) reported the species from several localities in British Columbia (Princeton on *P. ponderosa* and Cathedral Lakes on *Picea engelmanni*). Kelton (1977a) compared *A. lepidus* with the newly collected *A. pygmaeus* (Fallén) from Europe, a species found on *Pinus sylvestris* in Nova Scotia and New Brunswick. We report *A. lepidus* here from the Yukon Territory, Colorado, Oregon, and Wyoming.

**Specimens examined:** CANADA: British Columbia: Summit Lake, 16 August 1982, *P. c. latifolia*, 1 male (CNC); Yukon Territory, Rancheria, 11 August 1982, *P. c. latifolia*, 5 males, 1 female (CNC). UNITED STATES: Colorado: Gilpin Co., 3 km S Guanella Pass, 3,015 m, 4 September 1991, *P. c. latifolia*, 17 females; as before but *P. aristata* Engelm., 7 females; Larimer Co., 1 km SW Milner Pass, 3,298 m, R76W T5N, Rocky Mt. N. P., 3 September 1991, *P. c. latifolia*, 3 females. Oregon: Deschutes Co., Three Crks. Mdw., 26 km S Sisters, 2,000 m, 19 September 1979, *P. c. murrayana*, 1 female; Site 8, 6 August 1986, *P. c. murrayana* (trees 3, 19), 1 female, 1 male; Site 8, 26 August 1986, *P. c. murrayana* (general collecting) 1 female; Site 8, 20 August 1986, *P. c. murrayana* (tree 3), 1 female; Site 8, 3 September 1986, *Picea engelmanni* (10 trees pooled) 1 female. Wyoming: Albany Co., Site 2.1, 9 July 1986, *Pinus flexilis* (10 trees pooled), 3 males, 1 female; Site 2.1, 11 July 1986, *P. c. latifolia* (tree 15), 1 male; Site 2.2, 25 July 1986, *P. c. latifolia* (tree 18), 1 female; Site 2.1, 25 July 1986, *P. flexilis* (10 trees pooled), 11 females; Site 2.1, 5 September 1986, *P. flexilis* (10 trees pooled), 1 female; Site 3.1, 11 July 1986, *P. c. latifolia* (tree 16), 2 males; Site 3.1, 30 July 1986, *P. c. latifolia* (trees 2, 3, 6, 15, 16, 18, 20), 31 females; Site 3.1, 27 August 1986, *P. c. latifolia* (trees 5, 13, 16), 4 females; Carbon Co., Site 4.2, 17 July 1986, *P. c. latifolia*, 1 female. Park Co., Yellowstone Nat. Pk., 16.2 km N Norris, 2,277 m, 16 September 1980, *P. c. latifolia*, 3 females; Park Co., Yellowstone Nat. Pk., 1.6 km N Indian Crk. Cmpgd., 19.5 km N Norris, 2,270 m, 16 September 1980, *P. c. latifolia*, 2 females; Yellowstone Nat. Pk., 8.1 km S Tower Falls, 2,262 m, 17 September 1980, *P. c. latifolia*, 9 females.

#### *Anthocoris Fallén*

*Anthocoris Fallén*, 1814:9; Reuter, 1884:66; Lethierry and Severin, 1896:243; Van Duzee, 1917a:292; Collyer, 1953:86; Hill, 1957:171; Sands, 1957:296; Southwood and Leston, 1959:173; Anderson, 1962a:67; 1962b:1327; Anderson and Kelton, 1963:439; Cobben and Arnoud, 1969:5; Carayon, 1972a:345; Péricart, 1972:110; Herring, 1976:146; Evans, 1976a:85; 1976b:157; 1976c:163; 1976d:283; Kelton, 1978:34; Kerzhner, 1988:772; Henry, 1988:14.

**Diagnosis:** Length 2.4 to 4.6 mm, usually macropterous (except *A. dimorphicus* Anderson and Kelton); pruinose or shiny; dorsal pubescence; usually black or brown and white. Ocelli distinct; rostrum short, apex reaching or slightly surpassing front coxae. Pronotum with distinct collar and calli; lateral margin carinate. Hemelytra

smooth, pruinose or shiny. Hind coxae proximate. Ostiolar canal curved anteriorly, apical portion attached to metapleura, continued in anterior direction as a carina.

Approximately 30 species of *Anthocoris* are known, and most occur in the Northern Hemisphere (Lethierry and Severin, 1896; Péricart, 1972). Twelve species are known from North America (Henry, 1988). No recent world monograph for the genus exists. The best current treatment is that of Péricart (1972) who treats 14 species in the western Palearctic Region. No revision is available for North America, but Hill (1957) produced a key to the 11 species known to him. The best references to North American species are those of Anderson (1962b) and Kelton (1978).

Species of *Anthocoris* occur most commonly on broad-leaved plants, particularly on trees. Only two species in North America have been reported from conifers. They are searching predators, moving over the surface of the branches and leaves (Collyer, 1953; Sands, 1957; Southwood and Leston, 1959; Anderson, 1962a, b; Cobben and Arnoud, 1969; Péricart, 1972; Evans, 1976a, b, c, d; Kelton, 1978). Kelton (1978) listed host plants and summarized some of the literature dealing with five species considered important predators. A considerable literature on this genus documents the activities of the different species in agroecosystems (see e.g., Evans, 1976a, b, c, d).

*Anthocoris antevolens* White  
(Figure 2)

*Anthocoris antevolens* White, 1879:146; Reuter, 1884:77; Lethierry and Severin, 1896:243; Van Duzee, 1917a:293; b:262; Hill, 1957:172; Anderson, 1962b:1327; Anderson and Kelton, 1963:439; Kelton, 1978:37; Evans, 1983:45; Henry, 1988:14.

*Diagnosis:* Length 3.6–4.4 mm; macropterous, shiny; pubescence long and erect. Pronotum black, shiny, basal half usually pale brown. Hemelytra with clavus black except outer margin pale; basal third of corium and embolium pale, apical two-thirds of corium, embolium and all of cuneus black; membrane pale with middle and apical third fuscous.

*Habitat:* *Anthocoris antevolens* is an active, surface predator like *A. musculus* and other species of *Anthocoris*. Evans (1983) reported this species on *P. c. latifolia* in northwestern British Columbia. This species is a common predator in orchards (Anderson, 1962b; Wilde and Watson, 1963; McMullen and Jong, 1967; Kelton, 1978). According to Van Duzee (1917a) and Anderson (1962b), willow is the main host plant. Kelton (1978) added a number of host plants, mostly deciduous trees, including fruit crops where it feeds largely on Homoptera.

*Prey:* Anderson (1962b) reported aphids and mites as prey of *A. antevolens*. He documented this species biting humans, especially in orchards. Anderson and Kelton (1963) reported predation on several species of *Pemphigus* aphids on poplar and cottonwood and on the gall-forming aphid *Mordwilkoja vagabunda* (Walsh). Kelton (1978) reviewed some of the literature on the feeding habits of this species and noted that it feeds on psyllids (including the pear psylla) and mites. The reference to this species on *Pinus contorta latifolia* by Evans (1983) did not include prey records.

*Phenology and life history:* Anderson (1958, 1962b) detailed the life history of *A.*

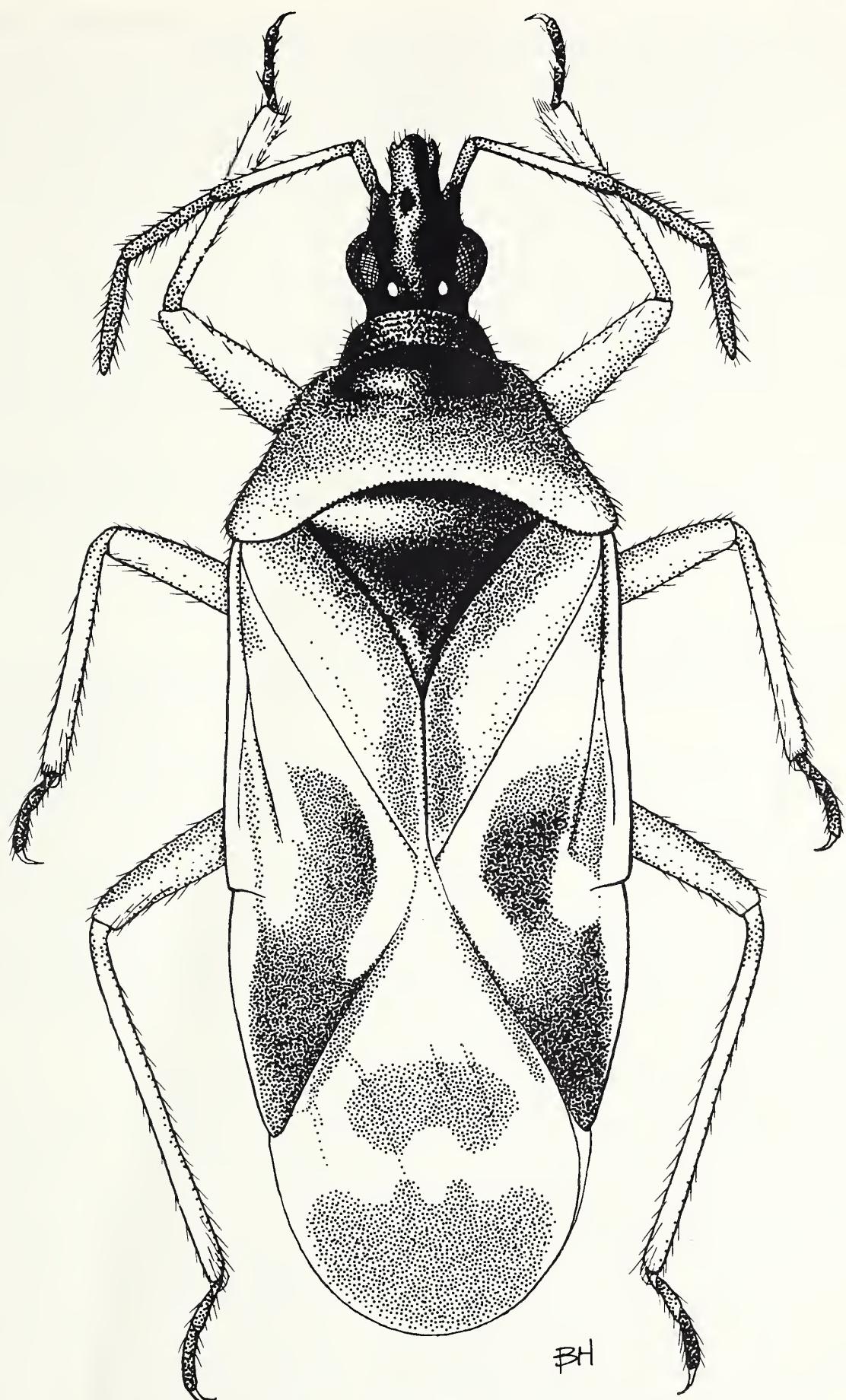


Fig. 2. *Anthocoris antevolens* White.

*antevolens*. Individuals, usually fertilized females, overwinter under bark scales and other parts of trees. The ratio of females to males was 8:1 in western Oregon. There appeared to be three generations per year in the Pacific Northwest, but four generations per year are possible in the laboratory. The egg stage lasts about 5 days. The duration of nymphal instars varies from 2.7 in the third- to 7.9 for fifth-instar females. Adults are long lived, especially the females. Under laboratory conditions, a mated female lived for 50 days. Naturally, the overwintering females live considerably longer.

*Distribution:* *Anthocoris antevolens* is widely distributed across Canada and northern United States, especially in the western part where it extends south along the coast into California, its type locality. Within the range of *P. contorta*, it has been recorded from Alaska, Alberta, British Columbia, California, Colorado, Idaho, Montana, Nevada, Oregon, and Wyoming. Much of its range overlaps that of *A. musculus*, with the former more prevalent in the west and the latter in the east.

*Specimens examined:* Many specimens from throughout the range of the species. The record of this species from *P. contorta latifolia* is that of Evans (1983) from British Columbia.

#### *Anthocoris musculus* (Say)

*Reduvius musculus* Say, 1832:32; Reuter, 1884:164.

*Anthocoris borealis* Dallas, 1852:588; Drake, 1921:202; 1922:66; Blatchley, 1926: 635.

*Anthocoris musculus*: Uhler, 1876:321; Lethierry and Severin, 1896:244; Van Duzee, 1917a:293; Strickland, 1953:199; MacPhee and Sanford, 1954:129; Reid, 1957: 111; Hill, 1957:172; Anderson, 1962b:1329; Anderson and Kelton, 1963:439; Kelton, 1978:40; Henry, 1988:14.

*Diagnosis:* Length 3.3–4.1 mm; macropterous, shiny; pubescence short and scattered, inconspicuous and appressed. Pronotum black, shiny; basal half pale colored, especially on postero-lateral angles. Hemelytra with clavus black, pale along outer margin; basal half of corium and embolium pale, apical half of corium, embolium and all of cuneus, black; membrane pale with dark pattern in middle and all of apical third.

*Habitat:* Kelton (1978) reported this species to be an active predator on a variety of surface-dwelling arthropods. Drake (1921, 1922) reported this species (as *A. borealis*) as an occasional visitor on conifers but stated it was more commonly found on deciduous trees, particularly on the branches and leaves of willow. He reported taking a few specimens under bark scales and in the burrows of bark beetles, including a few specimens from burrows of bark beetles on *Picea*. In England, Hamilton (1978) reported the occurrence of *A. nemorum* (L.), a similar species, under bark in the winter in England, often occurring with *Xylocoris*. Drake (1922) expanded his observations on *A. musculus* (as *A. borealis*), again noting its more common occurrence on willow where it feeds on lace bugs (Tingidae). Reid (1957) also reported *A. musculus* from the galleries of *Ips* in *Pinus contorta latifolia*. Kelton (1978) reported the species to be an active predator on a variety of surface-dwelling arthropods and added many additional host plants.

Anderson (1962b) reported it from alder and willow in British Columbia as do

two closely related species, *A. dimorphicus* Anderson and Kelton and *A. antevolens* (Anderson and Kelton, 1963; Kelton, 1978). Kelton (1978) added many other genera of deciduous plants as habitats and referred to its importance as a predator in orchards, especially apple orchards in eastern Canada. It appears that *A. musculus* is only an occasional visitor to conifers, although its occurrence in bark beetle galleries seems somewhat different from its usual surface-feeding habit.

*Prey:* Drake (1922) reported *A. musculus* feeding on several species of *Corythucha* (Hemiptera: Tingidae) on willow. Reid (1957) reported predation on eggs of *Ips* (*I. pini* Say and *I. perroti* Swain) on *P. contorta latifolia* in Alberta. It has been observed feeding on red mites (Kelton, 1978), the eyespotted bud moth in apple orchards in Nova Scotia (MacPhee and Sanford, 1954), and aphids (Strickland, 1953).

*Phenology and life history:* Little is known about this species except that it is a predator in orchards, particularly apple orchards, in eastern Canada (MacPhee and Sanford, 1954).

*Distribution:* Originally described from north-central United States, *Anthocoris musculus* is widespread from the Maritime Provinces of Canada west to British Columbia and Alaska and south to Oregon, Colorado, Kansas, Missouri, New York, and North Carolina. Part of its range overlaps that of *A. antevolens*.

*Specimens examined:* We have examined many specimens from throughout its range. The record for *Pinus contorta* is that of Reid (1957) from Alberta where it occurred in the galleries of *Ips pini* and *I. perroti* Swain. There are two specimens from Washington, Whatcom Co., Heather Meadows, R9E T39N Sec 19, 7 September 1979, *Abies amabilis*.

#### *Cardiastethus* Fieber

*Cardiastethus* Fieber, 1860:266; Van Duzee, 1917a:295; Herring, 1966:150; Péricart, 1972:249; Kelton, 1977a:246; Kelton, 1978:57; Henry, 1988:22.

*Diagnosis:* Macropterous, densely pubescent, long hairs on pronotum and hemelytra; antennal segments 3 and 4 hardly thinner than segment 2; pronotum punctate, lateral margin carinate; collar narrow, disc of pronotum with distinct transverse groove; ostiolar canal evenly curved forward and prolonged into carina that reaches anterior margin of metasternum. Male with single clasper, female with poorly developed ovipositor (Péricart, 1972; Herring, 1976; Kelton, 1978).

*Cardiastethus* is a cosmopolitan genus containing about 45 species (Péricart, 1972). Six species occur in the United States and Canada; all but one of these are found in the southern United States (Henry, 1988). A single species, *C. borealis* Kelton, is northern in distribution and may be the only species occurring on a conifer in North America. One European species, *C. fasciiventris* (Garbiglietti), occurs on conifers (*Abies* and *Picea*), but also is found on broad-leaf trees where it feeds on Psocoptera (Péricart, 1972). According to Southwood and Leston (1959), this latter species is mainly subcortical and overwinters as an adult. There is a single generation per year. Perris (cited in Péricart, 1972) reported nymphs from male flowers of pine in France. It will eat aphids in captivity. Another European species feeds upon scale insects.

*Cardiastethus borealis* Kelton  
(Figure 3)

*Cardiastethus borealis* Kelton, 1977a:246; Kelton, 1978:57; Henry, 1988:22.

**Diagnosis:** Small (2.25–2.70 mm), reddish-brown species, i.e., pronotum and hemelytra densely pubescent. Pronotum, scutellum and cuneus dark, most of wing pale. Habitus similar to species of *Orius*, but larger, brown rather than black, and more pubescent. Ostiolar canal distinctive, long and slender, evenly curved forward, terminal carina reaching anterior margin of metasternum. Single, sickle-shaped male clasper.

**Habitat:** Little information is available on the microhabitat of *C. borealis*. It has been collected on *Pinus ponderosa* in British Columbia, *P. banksiana* in Manitoba, and *P. sylvestris* in Nova Scotia (Kelton, 1977a, 1978). We record it here from *P. contorta latifolia* in central Oregon (Ochoco Mountains). *Pinus ponderosa* occurs at this locality in some abundance. The 1965 Oregon specimen, from northwest of Lakeview, lacked host information but probably occurred on *P. ponderosa* (J.D.L.).

**Prey:** No prey information is available for *C. borealis*. The single European species of *Cardiastethus* [*C. fasciiventris* (Gariglietti)] occurring on conifers (*Abies* and *Picea*), is reported to feed on Psocoptera (Péricart, 1972). A nonconifer inhabiting species in Europe is reported to feed on scale insects (Péricart, 1972).

**Phenology and life history:** Southwood and Leston (1959) reported that the British species of *Cardiastethus* overwinters as an adult. Perris (cited in Péricart, 1972) stated that the nymphs of *C. fasciiventris* occurred on the male strobili of pine in France. The early appearance of the adults on the strobili suggests they overwinter as adults or as eggs (e.g., most Miridae). The original type series (Kelton, 1977a) contained only a single male collected in early June in British Columbia. The other six specimens, all females, were collected in June (British Columbia and Manitoba) and July (Nova Scotia). The two specimens recorded here from central Oregon, a male and a female, were collected in July and August, respectively. Much remains to be learned about the habits of this species. Limited evidence suggests most species of *Cardiastethus* occur on deciduous trees: only two are found on conifers, one in Europe and the other in North America. *C. borealis* appears to occur on different hosts in different parts of its range.

**Distribution:** The type locality of *C. borealis* is Aspen Grove, British Columbia (Kelton, 1977a). Included in the type series were specimens from Seddon's Corner and Telford, Manitoba, and Mt. Uniacke, Nova Scotia. To these records we add two localities from central Oregon. A comprehensive systematic review of this genus is needed.

**Specimens examined:** Oregon: Crook Co., Ochoco Mts., Site 7, 9 July 1986, *Pinus c. latifolia* (tree 13), 1 male; Klamath Co.: L. Elder Ck., 48.7 km W Lakeview, 18 August 1965, 1 female.

*Elatophilus* Reuter 1884

*Elatophilus* Reuter, 1884:616; Blatchley, 1928:86; Sands, 1957:303; Southwood and Leston, 1959:173; Péricart, 1967:52; Biliotti and Riom, 1967:1103; Cobben and Arnoud, 1969:8; Carayon, 1972a:345; Péricart, 1972:97; Herring, 1976:146; Kel-

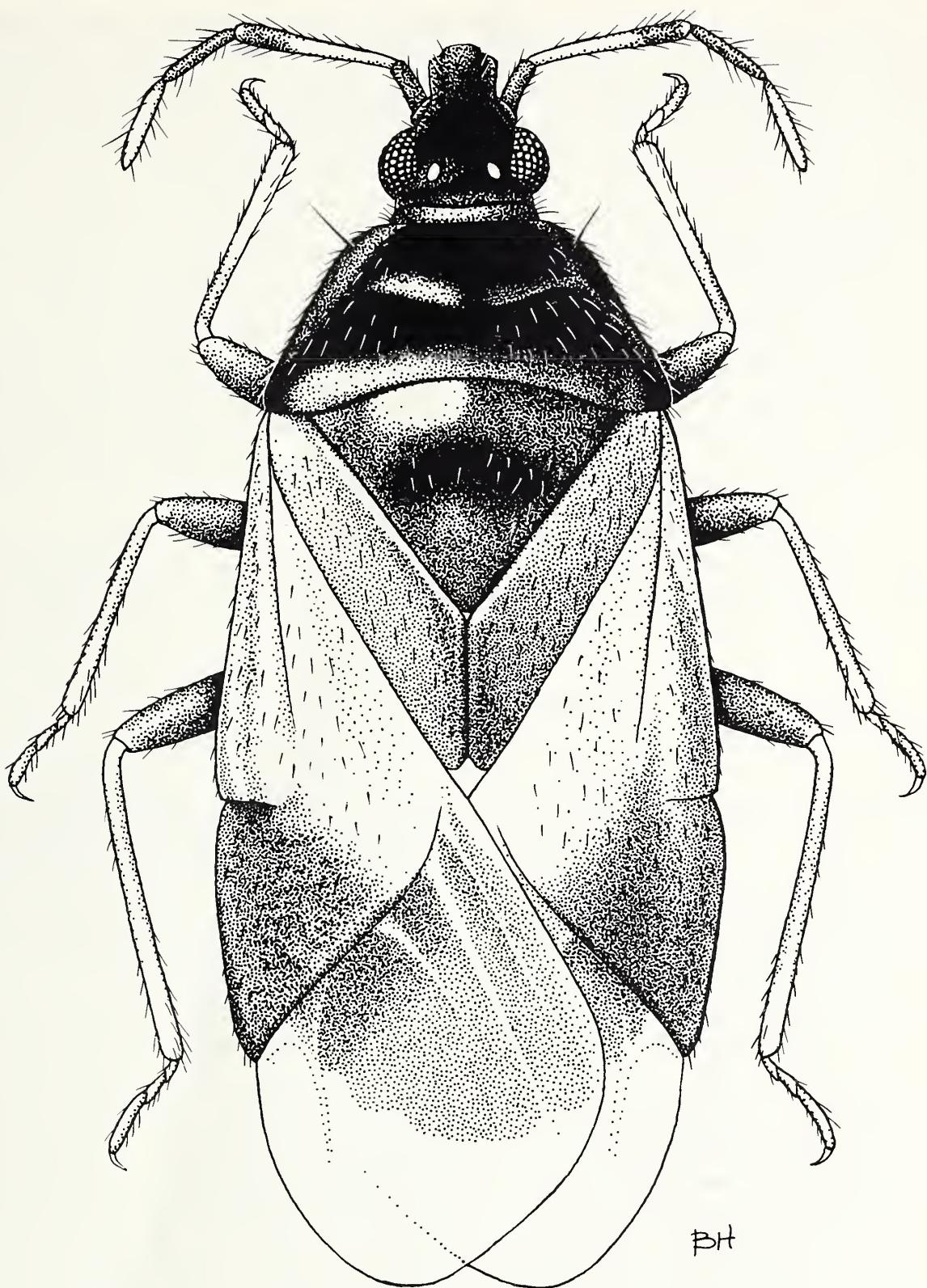


Fig. 3. *Cardiastethus borealis* Kelton.

ton, 1976b:631; Kelton, 1977b:1017; Kelton, 1978:19; Henry, 1988:15; Mendel, Carmi, and Podoler, 1991:502.

*Xenotracheliella* Drake and Harris, 1926:38 (Synonymized by Kelton and Anderson, 1962: 1306).

*Diagnosis:* Length 2.5–4 mm, flattened, usually dark with some pale markings, pubescence short. Head elongate, eyes prominent (especially in male). Antenna with

segment two linear or enlarged. Apex of rostrum extending to or beyond anterior coxae. Pronotum with poorly developed collar, dorsal surface roughened. Hemelytra dull, dark, usually marked with pale, macropterous or brachypterous (males and females), membrane with four veins. Ostiolar canal appressed to metapleuron, curved forward, apex rounded, hind coxae widely separated. Male clasper short, broad and curved.

*Elatophilus* Reuter contains 18 species distributed throughout the Holarctic Region, which are divided about equally between the Old and New World (Hiura, 1966; Péricart, 1972; Kelton, 1976b, 1977b, 1978; Mendel, Carmi, and Podoler, 1991). Seven of the eight described Nearctic species occur in America north of Mexico (Henry, 1988). Species of *Elatophilus* occur only on conifers and almost exclusively on the genus *Pinus* (Blatchley, 1928; Péricart, 1972; Kelton, 1976b; Mendel, Carmi, and Podoler, 1991). *Elatophilus* appears to be the conifer inhabiting analogue of the genus *Temnostethus* Fieber, a genus found on deciduous trees in the Palearctic (LeQuesne, 1955).

Where known, species of the genus *Elatophilus* appear to have a special relationship with species of the scale genus *Matsucoccus* Cockerell (Homoptera: Magarodidae) (Morrison, 1939; McKenzie, 1942a, b; Kosztarab and Kozar, 1988). Biliotti and Riom (1967) reported that *E. nigricornis* (Zett.) preyed on *Matsucoccus feytaudi* Duc., a pest of pine in France. These two authors cited unpublished observations of J. Carayon reporting the anthocorid from male strobili of *Pinus sylvestris* in the spring in France. Sands (1957) reported the same bug feeding only on aphids occurring on *P. sylvestris* in Britain. Cobben and Arnoud (1969) recorded *E. nigricornis* from The Netherlands and called attention to the discrepancy in the observed feeding reported by Sands with that of Biliotti and Riom. Cobben and Arnoud also pointed out the likelihood of associations between other species of *Elatophilus* and scales of the genus *Matsucoccus*. Péricart (1967) and Woodroffe (1969) described morphological differences among populations of *E. nigricornis* in Scotland and southern England. It is possible that such differences may extend to prey preference as well.

Mendel, Carmi, and Podoler (1991) summarized information on the 18 known species of *Elatophilus* and pointed out the presumed relations with species of the scale genus *Matsucoccus* and species of the conifer genus *Pinus*. Some corrections are needed on the information they provided for the eight North American species; these will be published elsewhere except for the species treated in our paper. They report confirmed observations of scale predation for five Palearctic and three Nearctic species, however, only *E. inimicus* (Drake and Harris) has been documented in North America as feeding on several species of *Matsucoccus* (Lussier, 1965).

In North America, Bean and Godwin (1955), Hartzell (1957) and Doane (1965) associated *E. inimica* with the red pine scale, *M. resinosa* Bean & Godwin, in New England. Lussier (1965) wrote a thesis on *E. inimica* and its role as a predator of the scale. He discussed the life history of this anthocorid in detail, and found a close correlation between the presence of the prey scale and the occurrence of the bug on the tree. Although Lussier found the anthocorid associated chiefly with *M. resinosa* on *P. resinosa*, he did cite one occurrence of the bug on *P. rigida* in association with *M. gallicolus* and on *P. sylvestris* in association with aphids and mites without the apparent presence of specimens of *Matsucoccus*. Drooz (1985) recorded the association of *E. inimica* with both species of *Matsucoccus* and summarized the life history

of both scale species. The anthocorid was first reported feeding on *M. resinosa* in plantations only outside the natural range of *Pinus resinosa*. Anderson, Ford, Kegg, and Risley (1976), among others, have suggested that *M. resinosa* may be an introduced species in North America since the scale is very abundant on plantations of the pine outside the tree's natural range.

Direct observations of predation upon species of *Matsucoccus* by species of *Elatophilus* have not been made in western North America. Several species of *Matsucoccus* occur on western species of pine, including *Pinus contorta*. Furniss and Carolin (1977) described host plants, seasonal history, and distributional information of the western species of *Matsucoccus*. Ray and Williams (1984) provided a key to North American species and gave additional host data. Anderson (1958) reported the association of *E. pullus* Kelton and Anderson (as *Elatophilus* sp. b) with the aphids *Essigella fusca* Gillette and Palmer and *Cinara* sp., and with the pine needle scale, *Chionapis (Phenacaspis) pinifoliae* (Fitch), on *P. ponderosa* in British Columbia. He reared *E. pullus* on the aphid *Myzocallis coryli* (Goeze) in the laboratory (1958, 1962b). We have encountered species of *Essigella* and *Cinara* on trees from which specimens of *Elatophilus* have been collected. A number of other potential predators of these aphids were taken at the same time, including Miridae and other species of Anthocoridae.

*Elatophilus dimidiatus* (Van Duzee)  
(Figure 4)

*Anthocoris dimidiatus* Van Duzee, 1921:139; Hill, 1957:173.

*Elatophilus dimidiatus*: Kelton, 1976b:632; Mendel, Carmi, and Podoler, 1991:503.

*Elatophilus (Elatophilus) dimidiatus*: Henry, 1988:15.

**Diagnosis:** Length 3.0 mm. Males macropterous, females macropterous or brachypterous; ocelli present in all forms and sexes. Head with apex of rostrum extending to middle of mesosternum. Basal half of hemelytra white or pale, including most of the clavus, corium, and embolium, apical half brown to black, wing membrane pale on basal half, dark brown to black on apical half; pubescence of wing moderately dense and long.

**Habitat:** Conventional beating of branches and small trees usually produced few specimens. Very rigorous beating with the edge of a straight axe handle produced more. Branches and trunks with scaly bark seemed most productive. The only recorded host for *E. dimidiata* is *Pinus contorta murrayana* (Grev. and Balf.) Engelm, the Sierra lodgepole pine (Little, 1979). Forrest (1980b) provided information about the monoterpenes of *P. contorta* oleoresin and defined some geographical areas based upon these chemical characteristics, including one he calls the Sierra Nevada Division that encompasses many of the collection sites of *E. dimidiatus*. All specimens that we have collected were beaten from the branches of *P. c. murrayana*.

**Prey:** Although Mendel, Carmi, and Podoler (1991) cite *Matsucoccus* spp. as the prey of *E. dimidiatus* no specific host prey have been observed or identified thus far. *Pinus contorta* hosts at least one species of *Matsucoccus*, its presumed prey, as well as the aphids belonging to *Cinara* and *Essigella*.

**Phenology and life history:** This species appears to overwinter as a nymph or an adult. The males seem to disappear much earlier than the females (see Péricart,

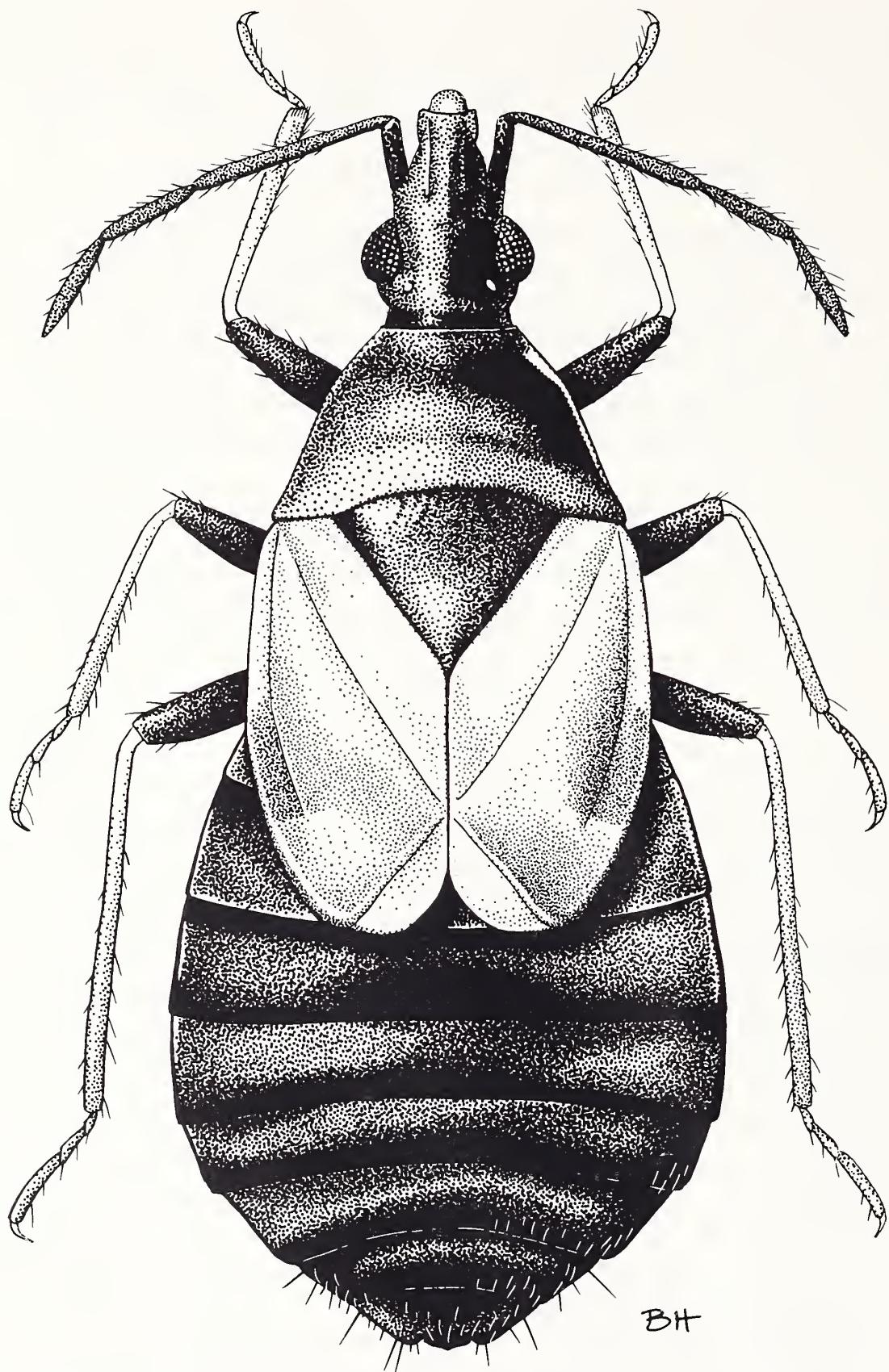


Fig. 4. *Elatophilus dimidiatus* (Van Duzee).

1967). Males and females were collected above Big Bear Lake, California, at an elevation of 2,215 m on June 8, 1989; a male was collected at an elevation of 2,954 m, west of Big Pine, California on June 6, 1989; brachypterous females were collected on June 23, 1981 at Childs Meadow, California (1,538 m) (Fig. 4); and the type series

(only females) from Cayton, California was collected on July 15, 1918. Near Sisters, Oregon; only females were collected on July 6, 1989.

*Distribution:* *Elatophilus dimidiatus* was described by Van Duzee (1921) (as a species of *Anthocoris*) from the Felch Ranch, near Cayton, Shasta Co., California based on three females. The type is mature and macropterous, the second specimen is teneral and macropterous, and the third, described by Van Duzee as a nymph, is actually a brachypterous female. As indicated in the section on wing polymorphism, species of this genus have always been regarded as macropterous in contrast to its deciduous tree analogue, *Temnostethus*. This brachypterous specimen of *E. dimidiatus* was subsequently included as a paratype of *Temnostethus fastigiatus* Drake and Harris (1926). In their paper (Drake and Harris, 1926), they erroneously cited the collection date of the specimen as 1913 rather than 1918. The taxonomic problems resulting from a mixed-type series will be dealt with in a subsequent publication.

As currently recognized, *E. dimidiatus* is known to occur above Big Bear Lake (San Bernardino Co., California); west of Big Pine (Mono Co., California); near Child's Meadow (Tehama Co., California); the type locality, Cayton (Shasta Co., California); and northward along the east side of the Cascade Mountains of Oregon at least as far as Sisters (Deschutes Co.). Brachypterous specimens, all females, are thus far known only from the San Bernardino, Tehama, and Shasta Co., California, localities.

*Specimens examined:* California: Mono Co., Cienega Mirth, 19.5 km W Big Pine, 6 June 1989, *Pinus c. murrayana*, 1 macropterous male; San Bernadino Co., above Big Bear Lake, end FS2N11, Champion tree site, R1W T2N NW ¼ Sec 34; 2,215 m, 8 June 1989, *P. c. murrayana*, 4 macropterous males, 12 brachypterous females; Tehama Co., Brokenshire Picnic area, 3.2 km W Child's Meadow, 1,754 m, 23 June 1981, *P. c. murrayana*, 3 brachypterous females. Oregon: Deschutes Co., Jct Hwy 20 and Metolius road, 1,077 m, 6 July 1989, *P. c. murrayana*, 6 macropterous females; 9.1 km NW Sisters, Hwy 20, 1,015 m, 26 August 1989, *P. ponderosa*, 2 macropterous females; as above, 14 September 1989, *P. ponderosa*, 1 macropterous female; as above, 26 September 1989, *P. ponderosa*, 2 macropterous females; 4.9 km S Sisters, 1,066 m, 14 September 1989, *P. ponderosa*, 1 macropterous female; as above, 24 September 1989, *P. ponderosa*, 1 brachypterous female; 14.6 km NW Sisters, Jct Hwy 20 and FS 2,060, 1,031 m, 6 July 1989, *P. c. murrayana*, 6 macropterous females; as above, 16 August 1989, *P. ponderosa*, 1 macropterous female; as above, 29 August 1989, *P. ponderosa*, 1 macropterous male, 1 macropterous female; as above, 14 September 1989, *P. ponderosa*, 2 macropterous, 1 brachypterous female; as above, 26 September 1989, *P. ponderosa*, 1 macropterous female.

*Elatophilus pullus* Kelton & Anderson  
(Figure 5)

*Elatophilus pullus* Kelton & Anderson, 1962:1306; Anderson, 1962b:1332; Kelton, 1978:22; Mendel, Carmi, and Podoler, 1991:503.

*Elatophilus* (*Elatophilus*) *pullus*: Henry, 1988:16.

*Diagnosis:* Length 2.6 to 3.0 mm. Males and females macropterous. Head with tip of rostrum reaching middle of mesosternum. Hemelytra dark, dull; bases of corium and embolium and middle of clavus often pale; membrane fumate, transparent; pubescence silvery, sparse, short and semi-erect.

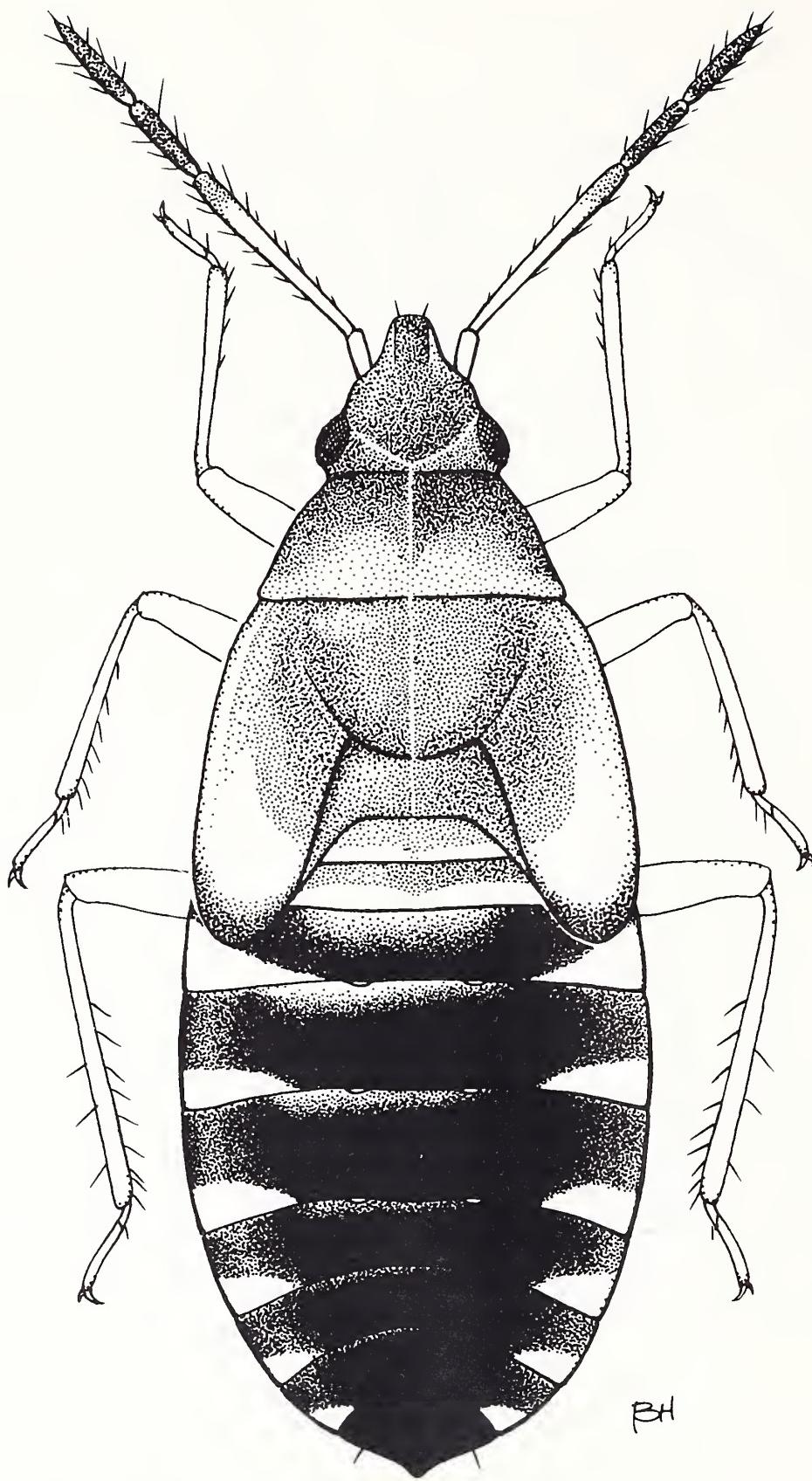


Fig. 5. *Elatophilus pullus* Kelton and Anderson.

**Habitat:** *Elatophilus pullus* occurs on *Pinus ponderosa* from British Columbia south to Oregon (Evans, 1983). The type series was collected from *P. ponderosa*. The exception is the John's Prairie, Washington site where we collected it from *P. contorta*. This locale, northwest of Olympia, is on the west side of the Cascade Mountains at the southern end of the Puget Sound. *Pinus ponderosa* occurs very rarely on the west

side of the mountains in Washington (Critchfield and Little, 1966). According to Forrest (1980b), the populations of *P. contorta contorta* in the Puget Sound area are discrete chemically and not particularly similar to the populations to the north or to the south. The trees looked more like the subspecies *P. c. murrayana* or *P. c. latifolia* than the coastal subspecies. No *Elatophilus* have yet been taken farther south from the coastal subspecies, *P. c. contorta*. Kelton (1978) lists *Pinus flexilis* James and *Picea glauca* (Moench) Voss as additional hosts.

**Prey:** Although the aphids *Essigella* and *Cinara* are taken regularly with *E. pullus* and other predatory Heteroptera, the relatively small numbers of the anthocorids collected suggest that the prey may be scale insects of the genus *Matsucoccus*. Furniss and Carolin (1977) provided host tree information on western species of *Matsucoccus* that differed from the scale species cited by Mendel, Carmi, and Podoler (1991) as possible prey for *E. pullus*.

**Phenology and life history:** According to Anderson (1962b), *E. pullus* overwinters as a fifth-instar nymph in the region around Summerland, British Columbia. Second and third instar nymphs were taken in mid-November and only fifth-instar nymphs were taken the following March. Males appeared first at the beginning of April, followed by the females about two weeks later. The males died within a month. Eggs were deposited during late April and hatched in early May. The occurrence of early instars in September suggested the possibility of a second generation. The series we collected from John's Prairie near Olympia, Washington, in early July from *P. contorta*, were all females. This bug has not yet been collected from the coastal form of *P. contorta* further south where we have collected extensively. In the vicinity of Sisters, Oregon, at an elevation of 1,046 m, we collected females of *E. pullus* on *P. ponderosa* on May 3, June 7, July 6, and August 2, 1989; fifth-instar nymphs from June 7 to August 16 (Fig. 5), and third-instar nymphs from July 6 to August 2, 1989. The early occurrence of females at this locale, and the absence of males suggests that fertilized females overwinter. A rather protracted generation may occur through the summer, with the males and females appearing in late August.

**Distribution:** *Elatophilus pullus* was described by Kelton and Anderson (1962) from specimens collected in British Columbia and Oregon. The type came from Westbank, British Columbia. Anderson (1962b) reported the species from Westbank and Summerland, British Columbia, and Adel, Chandler State Park, and Klamath Falls, Oregon, all from *P. ponderosa*. We have seen additional specimens from John's Prairie, near Shelton, Washington, and in the vicinity of Sisters, Oregon. With the exception of the John's Prairie record, all localities are on the east side of the Cascade Mountains from southern British Columbia, south to at least Klamath Falls, Oregon, near the Oregon-California border. At Sisters, Oregon, it occurs at the same locality as *E. dimidiata*, although on different host trees.

**Specimens examined:** CANADA: British Columbia: Summerland, 1 April 1958, *P. ponderosa*, 1 male; Summerland, 5 November 1957, lab reared ex *P. ponderosa*, 1 male; 16 km W Westbank, 26 June 1957, *P. ponderosa*, 1 female; Wilson's Landing, 14.6 km N Westbank, 6 May 1958, *P. ponderosa*, 2 females; as above, but 12 June 1956, 1 female. UNITED STATES: Oregon: Deschutes Co., 14.6 km NW Sisters, Jct Hwy 20 and FS 2060, 1,031 m, 7 June 1989, *P. ponderosa*, 1 female; as above, 20 July 1989, *P. ponderosa*, 1-IV instar nymph; as above, 16 August 1989, *P. ponderosa*, 1-V instar nymph; 4.9 km S Sisters, 1,066 m, 3 May 1989, *P. ponderosa*, 2 females; as above, 11 May 1989, *P. ponderosa*, 1 female; as above, 24 May 1989,

*P. ponderosa*, 1 female; as above, 7 June 1989, *P. ponderosa*, 1-IV instar nymph; as above, 2 August 1989, *P. ponderosa*, 1-II, 1-III instar nymphs; as above, 14 September 1989, *P. ponderosa*, 1 female; 9.1 km NW Sisters, Hwy 20, 1,015 m, 7 June 1989, *P. ponderosa*, 2-IV, 2-V instar nymphs; as above, 21 June 1989, 5-V instar nymphs; as above, 6 July 1989, 3 females; as above, 20 July 1989, 1-III, 1-IV instar nymphs; as above 2 August 1989, 1 female; as above, 16 August 1989, 3-V instar nymphs; as above, 26 September 1989, 2 females. Washington: Mason Co., John's Prairie, nr Shelton, 2 July 1988, *P. contorta*, 4 females. Wyoming: Park Co., Yellowstone Nat. Pk., 1.6 km N Indian Crk. Cmpgd., 19.5 km N Norris, 2,269 m, 16 September 1980, *P. contorta latifolia*, 2 females.

### *Elatophilus* sp. A.

An undescribed species of *Elatophilus* from *Pinus contorta* is referred to here as species A; it will be formally described when the generic revision of *Elatophilus*, now in progress, is completed. Species A may be separated from the other species of *Elatophilus* occurring on *P. contorta* by the enlarged second antennal segment. All specimens thus far collected have been macropterous.

*Habitat:* One specimen was taken on *Picea engelmanni* on Washington Pass, Washington; the other specimens have come from *Pinus contorta murrayana* in Oregon and northern California. No specific prey information is available other than the usual aphids beaten from the same hosts. Scale insects have not yet been collected from *P. contorta*, although at least one species of *Matsucoccus* is known to occur on it.

The specimens we collected were all females. The collection dates (from north to south) were Washington Pass, Washington, late September; southern Oregon Cascades, late June and mid-July; northern California, mid-July and mid-August. No nymphs have been collected that can be referred to this species with certainty.

*Distribution:* The species occurs in the Cascade Mountains from northern Washington (Washington Pass) south into northern California (near McCloud) and in the Sierra Nevada of California (near Calpine, Sierra Co.). Thus, it occurs in several different regions of *P. contorta murrayana*, as defined chemically by Forrest (1980b).

*Specimens examined:* California: Sierra Co., Plumas Nat. For., Hwy. 89, 5 km W Calpine, 1,631 m, 15 July 1987, *P. c. murrayana*, 1 female; Siskiyou Co., 24.4 km NNE McCloud, Swamp Creek Road and Hwy. 19, 14 August 1988, *P. c. murrayana*, 3 females. Oregon: Deschutes Co., 14.6 km NW Sisters, Jct 20 and FS 2060, 1,031 m, 6 July 1989, *P. c. murrayana*, 1 female; as above but 29 August 1989, 1 male; 14 September 1989, 1 female; 4.9 km S Sisters, 1,066 m, 14 September 1989, *P. ponderosa*, 1 male, 2 females; Harney Co., 16 km W Denio, 23 September 1959, 1 female; Klamath Co., 1.6 km W Crescent, 1,385 m, 17 July 1979, *P. c. murrayana*, 1 female; Klamath Co., nr Klamath Falls (above Geary Ranch), 26 June 1959, 1 female. Washington: Okanogan Co., Washington Pass, 1,615 m, 20 September 1979, *Picea engelmanni*, 1 female.

### *Lyctocoris* Hahn

*Lyctocoris* Hahn, 1836:19; Reuter, 1884:6; Van Duzee, 1917a:228; Sands, 1957:307; Kelton and Anderson, 1962:1302; Anderson, 1962b:1325; Kline and Rudinsky,

1964:8; Kelton, 1966b:320; Kelton, 1967:807; Chu, 1969:1; Carayon, 1972a:337; Péricart, 1972:200; Herring, 1976:149; Kelton, 1978:57; Dixon and Payne, 1979: 12, 13; Berisford, 1980:250; Goyer, Lenhard, Nebeker, and Schmitt, 1985:4; Kerzhner, 1988:770; Henry, 1988:23.

**Diagnosis:** Macropterous; length 3.30–4.90 mm; slightly flattened, shiny, pale to dark brown, pronotum and hemelytra punctate. Antennal segments three and four slender, setose; tip of rostrum reaching or exceeding middle coxae. Anterolateral margins of pronotum expanded, collar present and narrow, calli distinct. Hemelytra punctate and pubescent, four veins in membrane. Ostiolar canal slender, angulate, apex pointing forward. Left and right claspers present; ovipositor well-developed.

About 25 species of *Lyctocoris* have been described (Chu, 1969; Péricart, 1972); eight occur in the United States and Canada. The genus is distributed over much of the world. At least one species, *L. campestris* (Fabricius), is almost cosmopolitan, occurring very commonly in stored grain facilities. The extensive movement of grain throughout the world may be responsible for its wide distribution. This species also occurs in bird and mammal nests, hay stacks and thatch (Sands, 1957; Hicks, 1959). While largely predaceous on other arthropods in these habitats, it has been reported biting a person in New Zealand (Woodward, 1951; Anderson, 1962b). Anderson (1962b) reported it from a hen house, on apple trees, and in grain storage facilities. He recorded its occurrence under bark scales of maple and oak trees (fifth-instar nymphs and adults) during the winter in southern England. Moore (1972) reported *L. campestris* as a predator of the southern pine beetle. Kinzer (1976) reported this species from *Abies concolor* in New Mexico. This identification needs to be confirmed.

Dixon and Payne (1979) and Goyer, Lenhard, Nebeker, and Schmitt (1985) reported *L. elongatus* Reuter under pine bark in association with southern pine beetles, chiefly *Dendroctonus frontalis* Zimmerman but including three species of *Ips* as well. The species of *Ips* arrived slightly later to the trees than did *Dendroctonus frontalis*, and *Lyctocoris elongatus* (Reuter) showed a closer correlation with the *Ips* spp. than with *D. frontalis*. Kline and Rudinsky (1964) reported a *Lyctocoris* sp. as a possible predator of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins.

Kelton (1967) published a synopsis of the genus *Lyctocoris* for North America, providing information on the nine known species. He discussed the habits of some of the species treated. Most species are found under the bark of a wide variety of trees. Thus far, only a single species of *Lyctocoris* has been collected from *P. contorta*.

*Lyctocoris tuberosus* Kelton and Anderson  
(Figure 6)

*Lyctocoris elongatus*: Downes, 1927:11.

*Lyctocoris tuberosus* Kelton and Anderson, 1962:1303; Anderson, 1962b:1326; Kelton, 1967:812; Kelton, 1978:62; Evans, 1983:45.

*Lyctocoris* (*Lyctocoris*) *tuberosus*: Henry, 1988:24.

**Diagnosis:** Length 3.6 to 3.9 mm. Head and pronotum reddish brown, scutellum dark brown, hemelytra yellow brown tinged with reddish brown; membrane clear, outer vein well developed, other three faint; legs pale yellow brown. Tip of rostrum reaching hind coxae. Male with front and middle tibiae with a row of short, brown

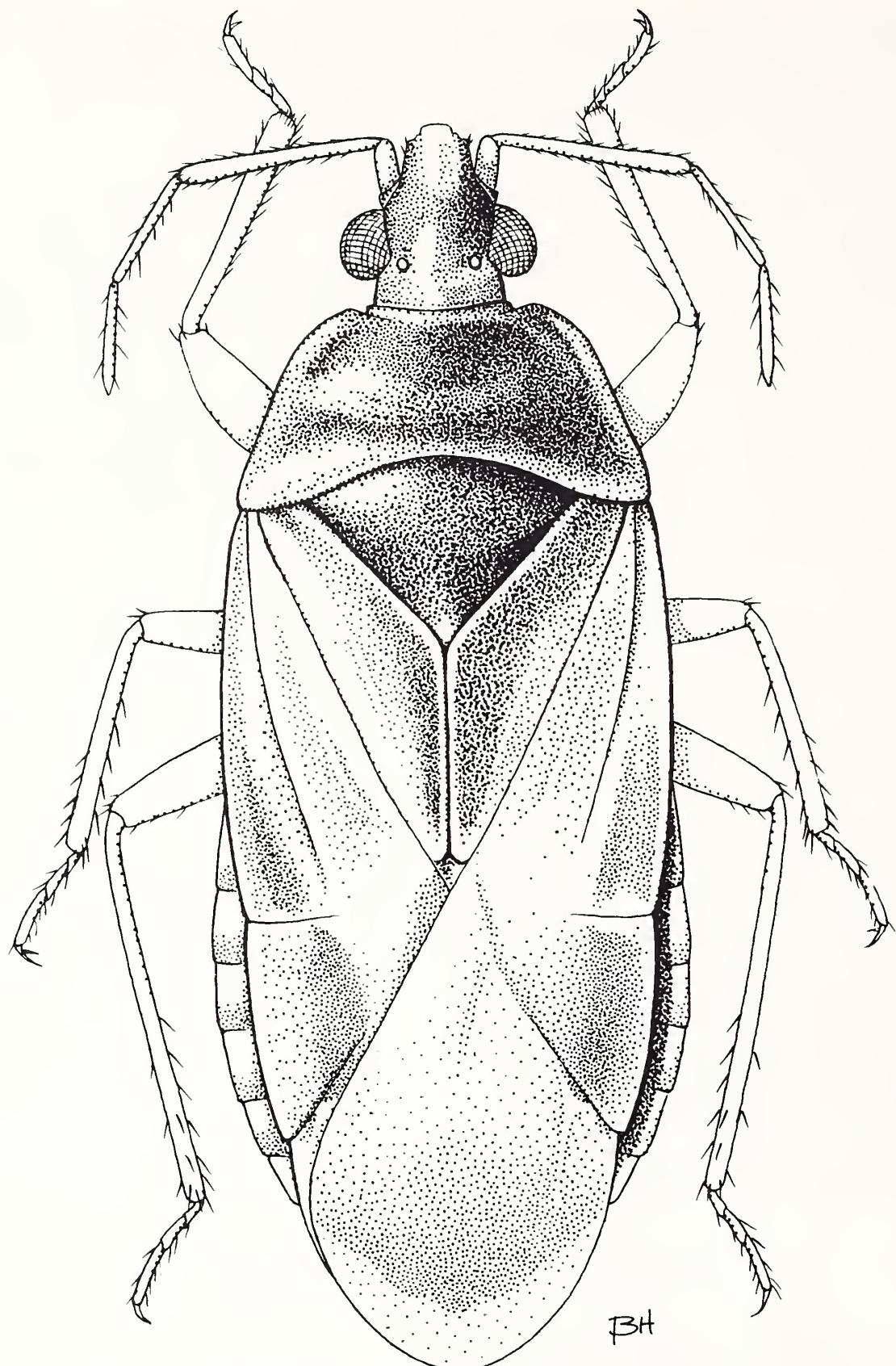


Fig. 6. *Lyctocoris tuberosus* Kelton and Anderson.

pegs on inner surface, hind tibiae with several long spines; abdominal segment seven with small tubercle on each side; left clasper flattened, apex obliquely truncate, right clasper smaller. Female with median portion of abdominal sternum six extended in posterior direction, inner margin of abdominal sternum seven gently curved, posterior margin almost straight, postero-medial angle rounded. Ovipositor well developed.

**Habitat:** Most records provide only host plants, but Kelton (1967) stated that the species occurs under the bark of *P. ponderosa*, *P. contorta*, and *Picea engelmanni* in association with bark beetles. Kline and Rudinsky (1964) reported *Lyctocoris* sp. from under the bark of *Pseudotsuga menziesii*, also in association with bark beetles.

The holotype was collected from *P. ponderosa* at Aspen Grove, British Columbia. Other host plants listed in the type series included *P. contorta* in British Columbia, *Picea engelmanni* in British Columbia, *P. ponderosa* in British Columbia and Colorado, and *Pinus monticola* in British Columbia. Anderson (1962b) added *P. ponderosa* in northeast Washington, *Pseudotsuga menziesii* (Mirbel) Franco in Oregon and *Pinus contorta* var. *latifolia* Engelmann in Oregon (note: this should be *P. c. murrayana*). Evans (1983) cited *P. ponderosa* as a host in southeastern British Columbia.

**Prey:** Kelton (1967) listed a species of the bark beetle genus *Ips* occurring on several species of *Pinus* and on *Picea engelmanni* as potential prey. Kline and Rudinsky (1964) cited a species of *Lyctocoris* as a possible predator of the Douglas-fir bark beetle, *Dendroctonus pseudostuga*, in the Pacific Northwest. Evans (1983) cited *L. tuberosus* as a "small active predator." Mosier, Thatcher and Pickard (1971) reported *L. elongatus* (Reuter) as an associate of *D. frontalis* and *Ips* spp. Goyer, Lenhard, Nebeker and Schmitt (1985) reported *L. elongatus* (Reuter) as a predator of southern pine bark beetles.

**Phenology and life history:** Very little is known about this species of *Lyctocoris*. Adults have been collected from April 28 through August 31 in southeastern British Columbia with both sexes being taken in late August. Specimens from southwestern Colorado were collected on April 23 (Kelton and Anderson, 1962). How any species overwinters is not yet known. No information is yet available on the immature stages.

**Distribution:** The type series contained specimens from Aspen Grove, Fernie, Lorna, Midday Valley, Merritt, Kane Valley and Trinity Valley, British Columbia, and from Pine River, La Plata Co., Colorado (Kelton and Anderson, 1962). Anderson (1962b) added Northport, Stevens Co., Washington, and Keno, Elsie and Pringle Falls, Oregon. He also stated the 1927 record of Downes of *L. elongatus* (Reuter) from Midday Valley, British Columbia, actually referred to a specimen of *L. tuberosus*. Kelton (1967) added South Dakota, with no specific locality. This is a widespread species, but with few known localities within that range.

**Specimens examined:** CANADA: British Columbia: Aspen Grove, 15 June 1933, *P. ponderosa*, #17480, lot 23, 1 female; Stanley, 26 June 1932, *Abies lasiocarpa*, #17424, lot 6, 1 female. UNITED STATES: Oregon: Jefferson Co., 3 km S Camp Sherman, 20 October 1962, under *P. ponderosa* bark, 1 female.

#### *Melanocoris* Champion

*Melanocoris* Champion, 1900:329; Van Duzee, 1917a:819; Kelton and Anderson, 1962:1307; Herring, 1976:144; Kelton, 1977a:246; Kelton, 1978:23; Henry, 1988:16.

**Diagnosis:** Macropterous; shiny; pubescence on hemelytra pale, flattened, scale-like or elongate and simple, may be serially arranged. Head short, tip of rostrum extending beyond anterior coxae; pronotum with collar indistinct, lateral margins broadly expanded; ostiolar canal short, straight, apex elevated; hind coxae widely separated, metasternum with apex straight or evenly rounded.

The genus *Melanocoris* contains four described species, all found in North America. The type of the genus is *M. obovatus* Champion, described from a female collected at Totonicapam, Guatemala (Los Altos region), between 8,500 and 10,500 feet, likely from a pine tree (Champion, 1900). The other three species occur in western Canada and United States (Drake and Harris, 1926; Kelton and Anderson, 1962; Kelton, 1978; Henry, 1988). Species of *Melanocoris* occur only on conifers, chiefly species of *Pinus* but occasionally on *Picea* and *Abies* (Champion, 1900; Van Duzee, 1921; Drake and Harris, 1926; Kelton and Anderson, 1962; Anderson, 1962b; Kelton, 1977a, 1978).

*Melanocoris longirostris* Kelton

*Melanocoris longirostris* Kelton, 1977a:246; Kelton, 1978:25; Henry, 1988:16.

*Diagnosis:* Length 2.60–3.00 mm, head and pronotum black, shiny; hemelytra brown, punctate, shiny, pubescence short and simple. Tip of rostrum extending beyond hind coxae.

*Habitat:* Kelton (1977a) reported *M. longirostris* from *Pinus monticola* in British Columbia; *P. ponderosa* and *P. strobiformis* in Arizona; and *Pinus flexilis*, *Picea glauca*, and *Abies lasiocarpa* in Colorado. We have collected it on *P. c. latifolia* and *P. flexilis* in Colorado; *P. c. murrayana* and *P. monticola* in Oregon; and *P. c. latifolia* and *P. flexilis* in Wyoming.

*Prey:* No specific prey information is available for this species. It was collected with woolly aphids on *P. monticola* in Corvallis, Oregon.

*Phenology and life history:* Adults have been collected in June, July, and August throughout the known range of the species. No specific life history information is available although both nymphs and adults were collected on July 25, and adults only on July 27 at site 2 in Wyoming.

*Distribution:* The species was described from a series of specimens collected at New Denver, British Columbia, and other localities in British Columbia, Colorado, New Mexico, Arizona and Utah. We add localities from eastern and western Oregon, Nevada, and southeastern Wyoming. The various host plants are listed under habitat.

*Specimens examined:* California: San Bernardino Co., above Wend Big Bear Lake, R1W T2W NW $\frac{1}{4}$  Sec 34, 2,215 m, 8 June 1989, champion *P. c. murrayana*, 3 females. Colorado: Larimer Co., Rocky Mt. Nat. Pk., 8.1 km W Estes Park, R13W T5N Sec 19, 2,677 m, 29 September 1990, *P. c. latifolia*, 1 female; Las Animas Co., 4 km S Cucharas Pass, 2,892 m, 5 September 1991, *P. aristata*, 1 female; Pitkin Co., 10 km S Aspen, 2,646 m, 11 September 1991, *P. c. latifolia*, 10 females, 1 male. Nevada: Washoe Co., Galena Cr., Mt. Rose, 14 June 1964, 1 female. Oregon: Benton Co., Corvallis, OSU campus, 1 July 1988 (teneral), *P. monticola*, 1 male, 1 female; Klamath Co., base of Gearhart Mt., 7 June 1959, *P. c. murrayana*, 1 female; Lane Co., H. J. Andrews Exp. For., 18 km NE Blue River, 18 August 1988, *P. monticola*, 2 males, 5 females, 2 V-instar nymphs. Wyoming: Albany Co., Sites 2.1 and 2.2, 25 July 86, *P. c. latifolia* adults and nymphs, 1 female; Site 2.2, 27 July 86, *P. c. latifolia* adults; Site 2.1, 9 July 86, *P. flexilis* (10 trees pooled), 1 female; Site 2.2, 25 July 86, *P. c. latifolia* (T-20), 1 female.

*Melanocoris nigricornis* Van Duzee  
(Figure 7)

*Melanocoris obovatus*: Van Duzee, 1917a:819, b:262.

*Melanocoris nigricornis* Van Duzee, 1921:143; Kelton and Anderson, 1962:1307; Anderson, 1962b:1332; Kinzer, Ridgill and Watts, 1972:10; Kelton, 1977a:246; Kelton, 1978:23; Henry, 1988:16.

*Tetraphleps novitus* Drake and Harris, 1926:41 (Colo.); Kelton and Anderson, 1962: 1307.

**Diagnosis:** Moderate length (2.66–3.50 mm), head, and pronotum black, base and margins of pronotum often brown; hemelytra dark brown, finely sculptured, shiny; pubescence on hemelytra scalelike and serially arranged. Tip of rostrum reaching anterior coxae.

**Habitat:** The original series was collected from pines in the southern part of the Sierra Nevada of California. One specimen was taken from Jeffrey pine (Van Duzee, 1921). Anderson (1962b) reported *M. nigricornis* from *Pinus ponderosa* and *P. c. latifolia* in British Columbia and *P. ponderosa* in Oregon. Kinzer (1976) reported *M. nigricornis* from *P. ponderosa* in New Mexico. Kelton (1978) reported the species from *Pinus sylvestris*, *P. contorta*, *P. ponderosa*, and *Picea engelmanni* in British Columbia. We add *P. c. murrayana* in Oregon, California, and Mexico, *P. c. latifolia* in Wyoming, and *P. radiata* in California.

**Prey:** *Melanocoris nigricornis* was collected in association with the aphids *Cinara* sp. and *Essigella fusca* G. & P., as well as the pine needle scale, *Phenacaspis pinifoliae* (Anderson, 1962b). Kelton (1978) speculated that the species probably feeds upon aphids, scales and other small arthropods. We collected aphids belonging to both *Cinara* and *Essigella* from the Oregon and Wyoming sites during 1986.

**Phenology and life history:** Adults have been collected from April (California and Mexico) to September (Oregon and Wyoming) in various parts of the range (Van Duzee, 1921; Drake and Harris, 1926; Anderson, 1962b; Kelton, 1978). According to Anderson (1962b), *M. nigricornis* overwinters as an adult in southern British Columbia and adults and nymphs were common from July to October. Reproduction continued into the fall with last instar nymphs collected in the latter part of October. Males and females were collected in early winter but only the females survived until spring. Under laboratory conditions, development from egg to adult took 24 days, and two consecutive generations were reared in the laboratory in only 67 days. Thus two generations are possible under field conditions.

**Distribution:** *Melanocoris nigricornis* was originally described by Van Duzee (1921) from three female specimens from California. One specimen was taken at Summit, Placer Co., at 2,154 m; another on pine trees on Mt. Tahquitz above Keen Camp, Riverside Co., at 2,154 m; the last was taken on Jeffrey pine at Monmouth, Mono Co. Previously, Van Duzee (1917a) reported this species (under the name *Melanocoris obovatus* Champion) from Summit, in Placer Co., California locality. *Tetraphleps novitus* was described by Drake and Harris (1926) from specimens collected in Colorado on pine at Stonewall and Trinidad, Las Animas Co., 2,770 m and Estes Park, Larimer County [note: *Pinus ponderosa scopulorum* is the common pine at these locales]. This species was synonymized with *Melanocoris nigricornis* by Kelton and

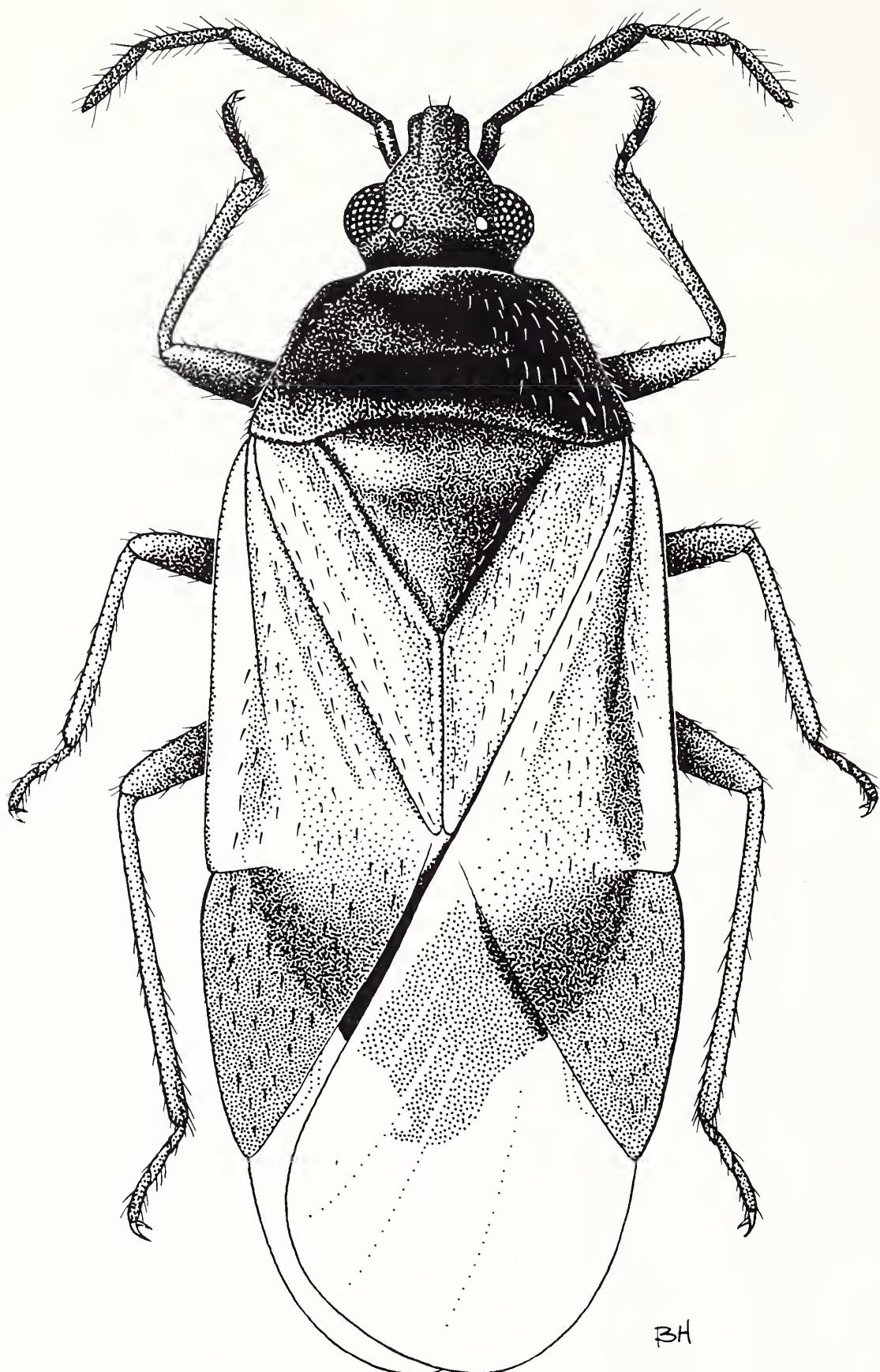


Fig. 7. *Melanocoris nigricornis* Van Duzee.

Anderson (1962). Anderson (1962b) reported *M. nigricornis* from several localities in the Okanagan Valley of British Columbia: Oliver to Westbank, Princeton, and from Adel, Oregon. Kelton (1978) reported it from several localities in southeastern British Columbia. We report here additional localities in Oregon and California and add Washington, Wyoming, and Mexico.

*Specimens examined:* CANADA: British Columbia: 19.5 km W Princeton, 1,169 m, 31 July 1957, *P. contorta*, 1 male. MEXICO: Baja California Norte, 90 km E San Telmo, 18 April 1979, *P. contorta*, 2 males, 4 females. UNITED STATES: California: Fresno Co., Pioneer Basin, 27 October 1959, 1 female (UCR). Mono Co., June Lake, Hwy. 158, 16 June 1989, *P. c. murrayana*. 3 females; Monterey Co., Pt. Lobos St. Res., E Hwy 1, Huckleberry Ridge Oak area, 8 April 1979, *P. radiata*, 1 female; Sierra Co., Tahoe Nat. For., off FS Rd. 07, 27.7 km W Hwy. 89, 2,092 m, 16 July 1987, *P. c. murrayana*, 1 female. Colorado: Larimer Co., Estes Park YMCA Camp, 6 km SW Estes Park, 2,465 m, R13W T4N Sec 4, 26 September 1990, *P. ponderosa scopularum*, 1 male, 3 females; Las Animas Co., 4 km S Cucharas Pass, 2,892 m, 5 September 1991, *P. ponderosa scopulorum*, 1 female. Oregon: Deschutes Co., Three Creeks Mdw., 26 km S Sisters, 2,065 m, 1 September 1977, *P. c. murrayana*, 3 males; Three Creeks Lake, 28 km S Sisters, 2,100 m, 14 June 1990, *P. c. murrayana*, 8 females; Black Butte Ranch, 13 km NW Sisters, 1,015 m, 24 March 1990, *P. sylvestris*, 3 males, 3 females; Linn Co., Big Lake, 1,431 m, 1 October 1979, *P. c. murrayana*, 4 females. Washington: Kittitas Co., 8 km W, 5 km S of Cle Elum, 6 June 1970, 1 female. Wyoming: Park Co., Yellowstone Nat. Pk., 8 km S Tower Falls, 2,262 m, 17 September 1980, *P. c. latifolia*, 3 females; Teton Co., Grand Teton Nat. Pk., 2,123 m, 18 September 1980, *P. c. latifolia*, 3 males.

### *Orius Wolff*

*Orius Wolff*, 1811:5; Carayon, 1953b:1206; Wagner, 1952:22; Carayon and Steffan, 1959:53; Kelton, 1963:631; Herring, 1966:1093; Carayon, 1972a:346; Péricart, 1972:160; Herring, 1976:147; Kelton, 1978:46; Henry, 1988:18.

*Triphleps* Fieber, 1860:266; Van Duzee, 1917a:293.

*Diagnosis:* Small, shiny, ovate, macropterous. Head short, ocelli distinct; tip of rostrum reaching anterior coxae; antennal segments II, III, and IV of equal thickness. Pronotum with punctures; short collar, not well differentiated; calli distinct, smooth. Hemelytra shiny, finely punctate, three veins in membrane. Anterior tibiae with fine, stout spinules on inner surface. Ostiolar canal curving forward, evaporative area broad and shiny.

More than 70 species of *Orius* are recognized and almost half of these occur in the Northern Hemisphere (Péricart, 1972). This is a large, complex genus with much additional work needed to achieve an understanding of the taxon. Wagner (1952) monographed the European species and recognized four subgenera. Kelton (1963) published a synopsis of the North American species, and Herring (1966) monographed the species of the Western Hemisphere. Carayon and Steffan (1959) reviewed the feeding habits of the genus. The North American fauna still requires additional work, for many of the described taxa are known from very few individuals. Two native species, *Orius insidiosus* (Say) and *O. tristiscolor* (White), are abundant throughout their respective ranges in North America, the former chiefly eastern and southern, and the latter northern and western (Kelton, 1963; Herring, 1966). Both have been deliberately introduced into Hawaii as biological control agents for two different Lepidoptera (Weber, 1953; Davis and Krauss, 1963). A selected bibliography of these two species was published by Ryerson and Stone (1979). A third species, *Orius minutus* (L.), represents an introduction into North America (Lattin, Asquith, and Booth, 1989).

*Orius tristicolor* (White)  
(Figure 8)

*Triphleps tristicolor* White, 1879:145; Van Duzee, 1914:15; Van Duzee, 1917a:293; b:262.

*Orius insidiosus* var. *tristicolor*: Blatchley, 1926:637.

*Orius tristicolor*: Harris and Shull, 1944:207; Anderson, 1962b:1330; Kelton, 1963: 634; Herring, 1966:1103; Kelton, 1978:50; Henry, 1988:19.

**Diagnosis:** Length 1.80–2.3 mm. Head black, shiny; tip of rostrum extending to anterior coxae. Pronotum black, shiny, punctate and rugose; calli smooth, raised. Scutellum black, shiny. Hemelytron with anterior half of corium, parts of clavus pale and shiny; balance of wing black; pubescence short, scattered; membrane fuscous, with two visible veins.

**Habitat:** Species of *Orius* occur on the surface of forbs, shrubs and trees including conifers. They are mobile predators that patrol the plant surfaces, feeding on small arthropods and their eggs (Collyer, 1953). Most species seem to be generalist predators, taking prey scaled to their size. *Orius tristicolor* has been found on a wide variety of plants and associated with many prey species (Anderson, 1962b; Ryerson and Stone, 1979). This species is often encountered in flower heads as well as on other parts of the plant.

Along with *O. insidiosus*, this is a ubiquitous species of Anthocoridae. Not primarily a conifer-inhabiting species, we have seen specimens from *Pinus ponderosa* (Oregon) and from *P. c. murrayana* (Baja California, Norte, Mexico). Their Oregon locality (near Sisters) had a scattered shrub understory of *Chrysothamnus* and *Purshia*.

**Prey:** *Orius tristicolor* feeds especially on Homoptera (Anderson, 1962b; Wilde and Watson, 1963; McMullen and Jong, 1967). However, Barber (1936) found that the early nymphal instars of *O. insidiosus*, a closely related species, were largely phytophagous and in fact could complete development on plant food alone. Dicke and Jarvis (1962) indicated that pollen is an important food source for *O. insidiosus*. Carayon and Steffen (1959) reported similar feeding habits for other species of *Orius*.

**Phenology and life history:** According to Anderson (1962b), this species overwinters as an adult (mostly females) and has been collected during winter from ground litter and has been beaten from deciduous and coniferous trees. He stated that three generations per year were likely in the Pacific Northwest but a fourth was possible. Developmental time from egg to adult was approximately 3 weeks. Eggs are inserted into leaves (including the veins) and hatch in about 7 days. Five instars occur with the duration of each stage about 4 days.

**Distribution:** The species ranges widely over Canada, northern and western United States, south through Mexico into Central and South America and the Bahamas (Kelton, 1963; Herring, 1966). In the eastern part of Canada and United States, it is largely replaced by *O. insidiosus*, which ranges through the southern and central states into Mexico and Central and South America and several of the West Indies (Kelton, 1963; Herring, 1966).

**Specimens examined:** Many specimens from throughout the range of the species. MEXICO: Baja California Norte, 90 km E San Telmo, 18 April 1979, *P. contorta*. UNITED STATES: Oregon: Deschutes Co., 4.9 km S Sisters, 26 September 1989, *Pinus ponderosa*, 2 females; Linn Co., Big Lake, 1,431 m, 1 October 1979, *P. c. murrayana*, 1 female.

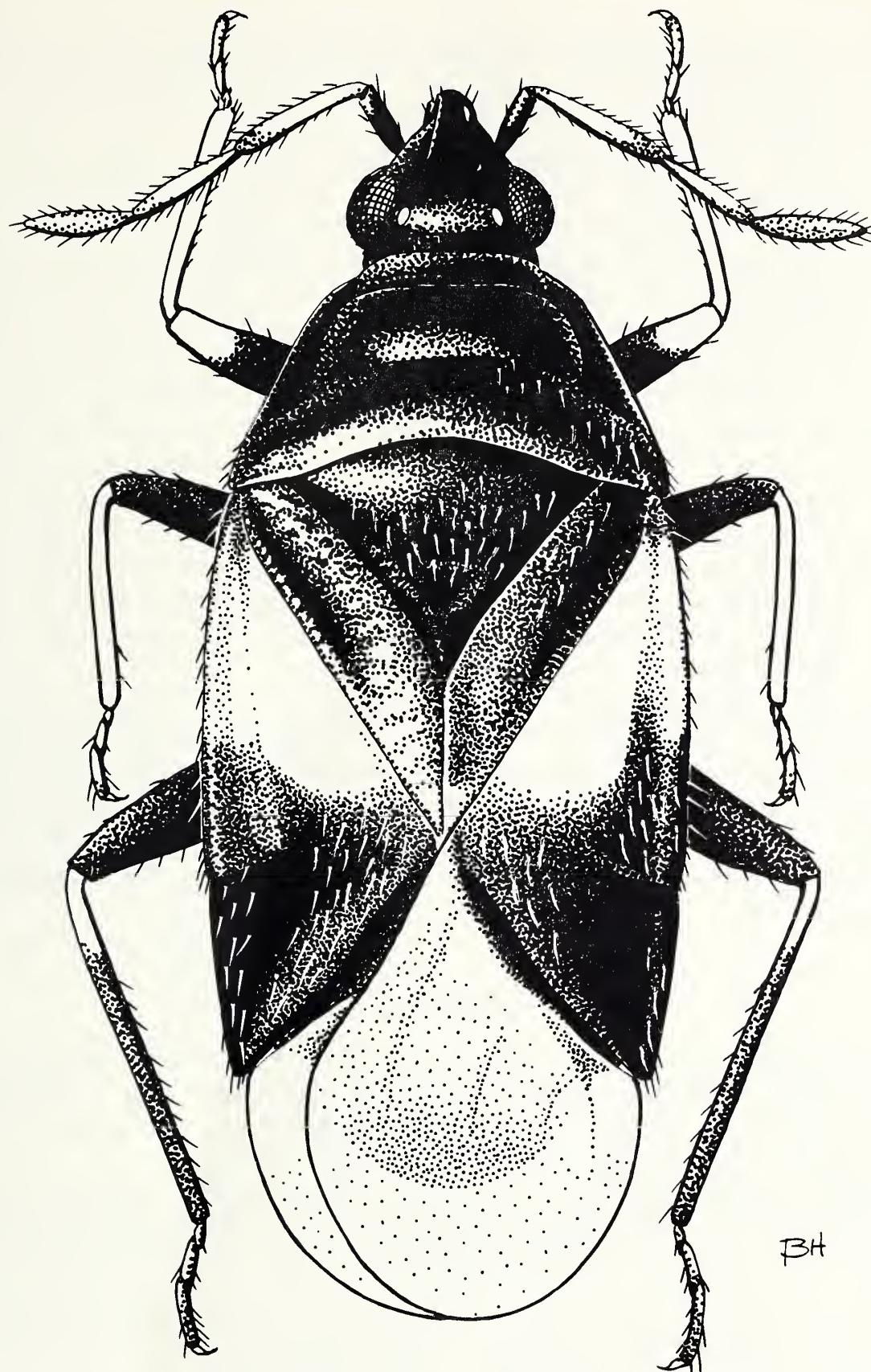


Fig. 8. *Orius tristiscolor* (White).

*Scoloposcelis* Fieber

*Scoloposcelis* Fieber, 1864:62; Van Duzee, 1917a:296; Carayon, 1953a:65; Carayon, 1972a:341; Péricart, 1972:279; Kelton, 1976a:196; Herring, 1976:149; Kerzhner, 1988:771; Henry, 1988:25.

*Diagnosis:* Body flattened, sides subparallel, smooth, shiny. Macropterous, corium, and clavus impunctate. Legs stout, anterior and posterior femora enlarged, anterior femur with short, stout teeth on inner surface. Long setae at end of abdomen. Male clasper short, stout, slightly curved, parallel-sided except apex.

Twelve species of *Scoloposcelis* are known, nine in the Holarctic Region (Péricart, 1972). Two species, *S. flavigornis* Reuter and *S. basilicus* Drake and Harris, are known from America north of Mexico (Henry, 1988). The former species occurs throughout the United States and Canada from Mississippi and Texas to the Yukon Territory, whereas the latter is known only from Arizona and New Mexico. It is likely that additional species will be recognized. Species of *Scoloposcelis* occur under the bark of conifers, chiefly species of the genus *Pinus* where they feed mainly on Scolytidae and other subcorticular insects (Drake, 1921, 1922; Carayon, 1953a; Mosier, Thatcher, and Pickard, 1971; Péricart, 1972; Moore, 1972; Goyer, Lenhard, Nebeker, and Schmitt, 1985). Carayon (1953a) provided a detailed discussion of the habits and habitats of *S. obscurella* (Zett.). The range of this species extends from Europe to the far-eastern U.S.S.R. (Kerzhner, 1988). Carayon stated that the species occurs not so much under bark, but between the layers of bark where its exceptionally flat shape permits it to enter crevices most insects could not. Besides scolytids, Carayon reported that *S. obscurella* fed upon the larvae of *Tribolium*, *Gnathocerus*, *Anobium* and *Oryzaephilus* in captivity.

Carayon (1953a) described the life cycle of *S. obscurella* in France. Eggs deposited in tree bark hatch in about 12 days. The resulting nymphs are reddish, and gradually darken as they become older. The nymphs are distinctive in appearance: very flat, parallel-sided, with the anterior and posterior femora greatly enlarged. The anterior pair have a row of short teeth on the inner surface. Several very long setae extend from the end of the abdomen. There are five nymphal instars and a single, protracted generation per year.

*Scoloposcelis flavigornis* Reuter  
(Figure 9)

*Scoloposcelis flavigornis* Reuter, 1871:561; Van Duzee, 1917a:297; Drake and Harris, 1926:44; Harris and Shull, 1944:207; Anderson, 1962b:1332; Kelton, 1976a:196; Kelton, 1978:52; Berisford, 1980:250; Dixon and Payne, 1979:13, 25; Ohmart, 1981:5; Ohmart and Voight, 1981:677, 680; Henry, 1988:25.

*Scoloposcelis mississippiensis* Drake and Harris, 1926:45 (Miss.); Mosier, Thatcher and Pickard, 1971:73; Moore, 1972:63; Kelton, 1976a:196; Dixon and Payne, 1979:13, 25; Berisford, 1980:250; Goyer, Lenhard, Nebeker, and Schmitt, 1985:4.

*Scoloposcelis occidentalis* Drake and Harris, 1926:45 (Calif.); Kelton, 1976a:196.  
*Anthocoris* sp.: Drake, 1921:201; Drake, 1922:67; pl. II, fig. b.

*Diagnosis:* Body elongate, parallel-sided and very flat; dorsum shiny, glabrous; anterior and posterior femora enlarged, anterior femur with short teeth on inner surface. Several long setae at end of the abdomen. Head and pronotum dark, shiny; macropterous, hemelytra shiny, glabrous; clavus and corium largely pale, dark along claval suture, embolium and most of cuneus, with membrane clear.

Some morphological differences in some of the specimens examined suggest the likelihood of at least one other species, perhaps a northern and southern species.

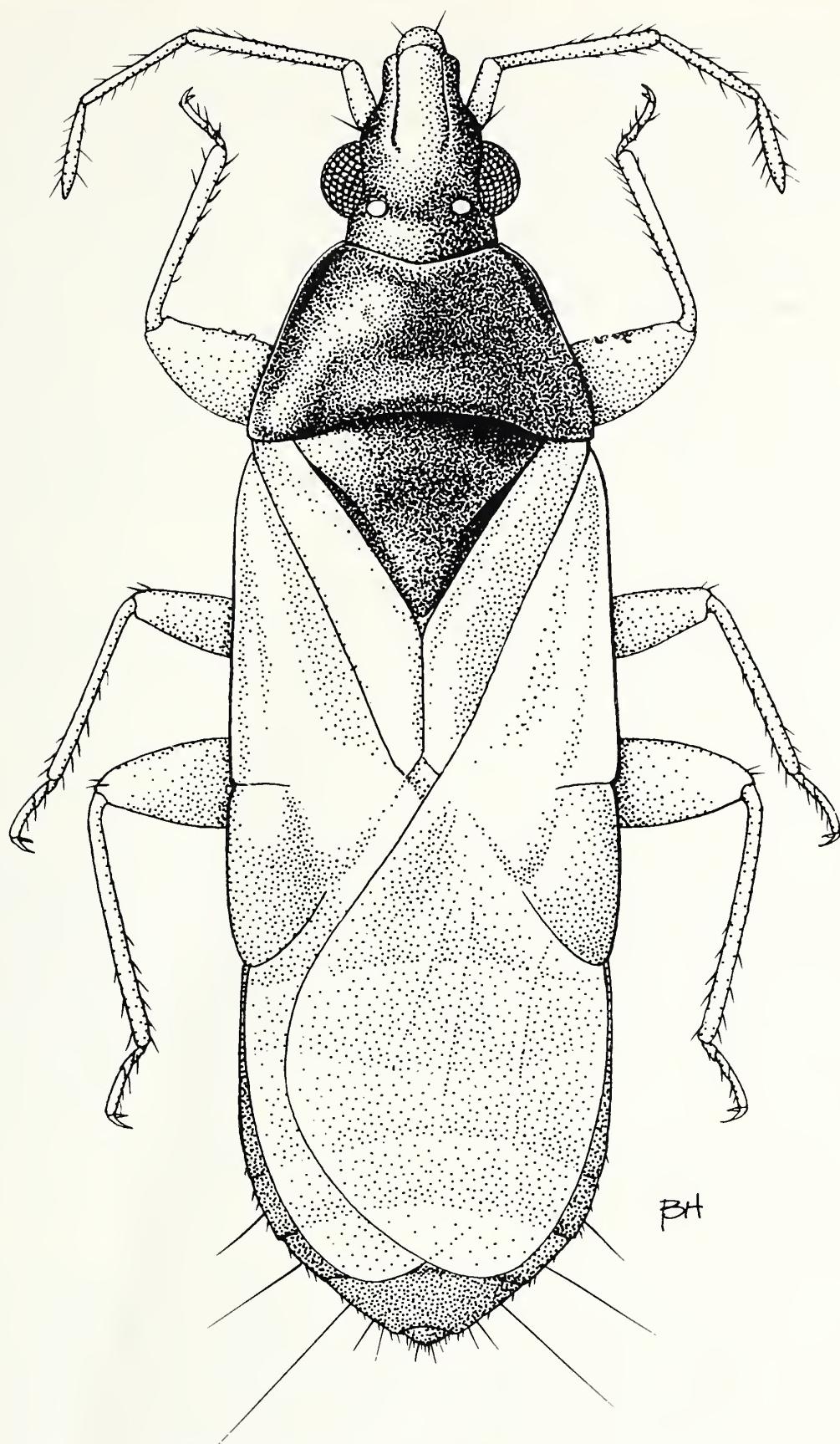


Fig. 9. *Scoloposcelis flavigornis* Reuter.

Only a thorough examination of available specimens will clarify this situation. Because both *S. obscurella* Zett. and *S. pulchella* Zett. have been reported from the far-eastern Palearctic Region by Kerzhner (1988), specimens from the far northwestern portion of North America should be examined with special care.

**Habitat:** *Scoloposcelis flavigornis* occurs under the bark of trees where it is often found in the burrows of bark and ambrosia beetles (Drake, 1921, 1922; Drake and Harris, 1926; Dahlsten, 1970; Mosier, Thatcher, and Pickard, 1971; Moore, 1972; Kelton, 1976a; Dixon and Payne, 1979; Ohmart and Voight, 1981; Ohmart, 1981; Goyer, Lenhard, Nebeker, and Schmitt, 1985). We collected adults of *S. flavigornis* in the Cascade Mountains of Oregon in July beneath bark flakes of a recently dead branch of *P. c. murrayana* (needles brown, attached) together with three species of Scolytidae. Fifth-instar nymphs were collected from *P. resinosa* at Harvard Forest (near Petersham), Massachusetts, in mid-October. These specimens were beaten from dead branches on the ground that had been cut earlier in the year (needles brown, attached). Only branches with scaly bark produced specimens. By mid-November, the specimens were still in the nymphal state. The Oregon record of *S. flavigornis* is based on specimens from a subalpine meadow at 2,000 m on the east side of the Cascade Mountains on *P. c. murrayana* in mid-July. This is in contrast to the Washington specimens taken at Bremerton, Washington, just west of Seattle at sea level from shore pine (*P. c. contorta*).

This species has been collected from *Pinus contorta contorta*, *P. c. latifolia*, *P. c. murrayana* (this paper), *P. banksiana* (Kelton, 1978), *P. palustris* (Drake and Harris, 1926), *P. ponderosa* (Dahlsten, 1970; Kelton, 1978), *P. radiata* (Ohmart and Voight, 1981; Ohmart, 1981), *P. resinosa* (Kelton, 1978), *Picea glauca* (Kelton, 1978), and *Picea* sp. (Drake, 1921, 1922).

**Prey:** The chief prey of *S. flavigornis* appears to be the eggs and larvae (and perhaps callow adults) of Scolytidae. Drake (1921, 1922) reported it (as *Anthocoris* sp.) from the burrows of 11 species of bark and ambrosia beetles in spruce logs in New York and reported feeding on both types of beetles. He provided an excellent drawing of the fifth-instar nymph, showing the characteristically enlarged front and hind femora. Drake and Harris (1926) reported nymphs and adults (as *S. mississippiensis*) in the burrows of *Ips* spp. in long-leaf pine. Dahlsten (1970) reported likely predation on *Dendroctonus brevicomis* LeConte in California. Mosier, Thatcher, and Pickard (1971) reported *S. flavigornis* as a predator of the eggs and larvae of *Dendroctonus frontalis* Zimmerman and *Ips* sp., as did Moore (1972). Ohmart (1981) reported it from the brood gallery of *Ips paraconfusus* Lanier, while Dixon and Payne (1979) and Goyer, Lenhart, Nebeker, and Schmitt (1985) recorded it as an associate of *D. frontalis*. According to the latter, another anthocorid, *Lyctocoris elongatus* Reuter, occurred with *S. flavigornis*.

**Phenology and life history:** Winter is normally spent as a mature nymph (at least in northern locales). Adults appear in the spring and usually disappear in early fall. Carayon (1953a) provided a detailed account of *S. obscurella*, collected in the mountains of central France, and the general phenology was the same. The original description of *S. mississippiensis* (Drake and Harris, 1926) mentioned males, females, and fourth and fifth-instar nymphs being collected together at Port Gibson, Mississippi, on *Pinus palustris* in late July. Mosier, Thatcher and Pickard (1971) reported the occurrence of *S. flavigornis* (as *S. mississippiensis*) in January and March through November. Dixon and Payne (1979) showed a close correlation between the arrival of *Scoloposcelis* and the bark beetles, especially *Dendroctonus frontalis*, attacking pines in southern United States. The beetles are multivoltine and it appears that the anthocorid is too, thus explaining the occurrence of the bug throughout the year.

Ohmart (1981) stated that *S. flavigornis* was collected throughout the year on *Pinus radiata* in coastal California, but was most abundant from November to March. He did not indicate life stages collected.

**Distribution:** *Scoloposcelis flavigornis* was described from Texas by Reuter (1871). This widespread anthocorid has since been recorded from Alberta, British Columbia, California, Florida, Idaho, Indiana, Manitoba, Mississippi, New Brunswick, Nova Scotia, Ontario, Pennsylvania, Quebec, Saskatchewan, Yukon Territory, Guatemala, and Mexico (Henry, 1988). To these records we add Oregon, Massachusetts and Washington. Two species described by Drake and Harris (1926), *S. mississippiensis* from Mississippi and *S. occidentalis* from Ventura Co., California, were synonymized with *S. flavigornis* by Kelton (1976a).

**Specimens examined:** Massachusetts: Worcester Co., Harvard Forest, nr Petersham, 28 September 1989, under bark of dead branches of *Pinus resinosa*, five fifth instar nymphs. Montana: Ravalli Co., Sula, 26 June 1929, *Pinus contorta latifolia*, Hopk. US/19509, 7 males, 2 females (USFS, LaGrande, Ore.); Sula, 8 July 1929, *Pinus contorta latifolia*, Hopk. US/19509, 6 males, 1 female (USFS, LaGrande, Ore.); Sula, 27 July 1929, *Pinus contorta latifolia*, Hopk. US/19509, 7 males, 2 females (USFS, LaGrande, Ore.) Oregon: Deschutes Co., Three Creeks Meadow, 2,069 m, 26 km S Sisters, 11 July 1988, under bark of dead branch of *P. c. murrayana* together with three species of Scolytidae, 2 males, 6 females. Washington: Kitsap Co., Bremerton, 17 February 1975, emerged indoors, 19 February from gallery of *Pityophthorus confertus*, in *P. c. contorta*, 1 female.

#### *Tetraphleps* Fieber 1860

*Tetraphleps* Fieber, 1860:262; Reuter, 1884:56, 85; Lethierry and Severin, 1896:245; Reuter, 1908:86; Parshley, 1920:83; Van Duzee, 1921:143; Drake, 1921:203; 1922: 67; Drake and Harris, 1926:41; Kelton and Anderson, 1962:1307; Anderson, 1962b: 1331; Ghauri, 1964:675; Kelton, 1966a:199; Mitchell and Wright, 1967:143; Harris, Holms, and Dawson, 1968:5–6; Kelton, 1968:1072; Carayon, 1972a:345; Péricart, 1972:154; Herring, 1976:146; Kelton, 1978:26; Evans, 1983:45; Kerzhner, 1988: 771; Henry, 1988:17.

**Diagnosis:** Macropterous, shiny, pubescent. Tip of rostrum reaching or exceeding front coxae. Pronotum with distinct collar, lateral margins carinate, calli smooth, surface punctate. Hemelytra with punctures, shiny, pubescent, membrane with four veins. Hind coxae close together. Ostiolar canal straight, apex rounded, raised above surface of metapleuron.

The genus *Tetraphleps* contains approximately 12 species (Péricart, 1972). The species occur in the Northern Hemisphere, with about equal numbers in the Old and New World. Five species are known to occur in North America (Kelton, 1966a, 1978; Henry, 1988). Keys to the North American species are found in the two papers by Kelton (1966a, 1978), together with information on distribution and host associations. Species of *Tetraphleps* are found only on conifers, especially of the genus *Pinus*, and to a lesser extent on *Larix*, *Picea*, *Abies*, and *Pseudotsuga* (Reuter, 1908; Péricart, 1972; Kelton, 1978). Kinzer, Ridgill, and Watts (1972) and Kinzer (1976) recorded *Tetraphleps* sp. from *Pinus ponderosa* cones in New Mexico. Evans (1983) reported *Tetraphleps* sp. from lodgepole pine in the northern interior of British Columbia.

Species of *Tetraphleps* are active, surface feeding predators, often abundant on their host plants. Their main food seems to be aphids. Péricart (1972) mentioned several aphids of the genus *Cinara* as primary prey of *T. biscuspis* (H.-S.) in Europe. *Cinara* spp. were commonly collected from *P. c. murrayana* and *P. c. latifolia* at a number of localities in the present study. Specimens of the aphid genus *Essigella* also were taken.

Mitchell and Wright (1967) reported the introduction of *Tetraphleps* spp. from Pakistan and India in 1964. Specimens from Pakistan were released at Randle, Washington, and Portland, Oregon (Hoyt Arboretum), and those from India at Wind River, Washington (Wind River Arboretum), and into a laboratory culture. It is not known if they have become established (Dr. R. G. Mitchell, pers. comm., 12 March 1990). These anthocorids were released as potential predators of the balsam woolly adelgid, *Adelges piceae* (Ratzeburg). These same species, ultimately identified as *Tetraphleps abdulghani* Ghauri from Pakistan, and *T. raoi* Ghauri from India (Ghauri, 1964; Henry, 1988), were introduced onto Vancouver Island (Thetis Park), British Columbia in 1965 (Harris, Holms, and Dawson, 1968). According to Dr. L. M. Humble, Forest Insect and Disease Survey, Forestry Canada, Victoria, British Columbia, these species apparently have not become established (pers. comm., 2 March 1990). According to Kelton (1978), they were also introduced into New Brunswick and Nova Scotia, and as of 1971, had not been recovered. Two native species, *T. latipennis* Van Duzee and *T. sp.*, were collected at the Thetis Park release site in 1964 and 1965.

A shortage of specimens from a number of localities makes it difficult to assess the degree of species variation. Females predominate in most collections, mainly because of the timing of collections; and thus the variation in male genitalia, especially the claspers, is largely unknown. A thorough revision of *Tetraphleps*, with examination of all type material, almost certainly will result in the recognition of additional species.

#### *Tetraphleps canadensis* Provancher

*Tetraphleps canadensis* Provancher, 1886:90; Parshley, 1920:85; Van Duzee, 1921: 142; Drake and Harris, 1928:50; Anderson, 1958:50; Kelton and Anderson, 1962: 1307; Anderson, 1962b:1331; Kelton, 1966a:199; Kelton, 1968:1072; Kelton, 1978: 27; Henry, 1988:17.

*Lyctocoris canadensis*: Van Duzee, 1912:320.

*Tetraphleps americana* Parshley, 1920:84; Drake and Harris, 1928:50.

*Tetraphleps osborni* Drake, 1922:67; Kelton and Anderson, 1962:1307.

*Acompocoris (Tetraphleps) osborni*: Drake and Harris, 1926:43.

*Tetraphleps edacis* Drake and Harris, 1926:43; Kelton and Anderson, 1962:1307.

*Diagnosis*: Length 3.1 to 3.9 mm. Head, pronotum and scutellum black, shiny, pubescence dense and rather long. Hemelytra pale brown, shiny, finely punctate, with rather long, dense pubescence. Apex of rostrum reaching middle of mesosternum. Hind tibiae with short setae. Ostiolar canal with posterior margin concave, apex broadly rounded.

*Habitat*: Drake (1921) reared a specimen (as *Tetraphleps* n. sp.) from the burrows of a weevil from Bebb's willow (*Salix bebbiana* Sarg.) in New York, but he thought

that pine was its usual host. Drake (1922) mentioned it (as *Tetraphleps osborni*) was a predator of leaf-feeding insects on *Pinus strobus* in New York. Drake and Harris (1926) reported *Larix laricina* as a host (as *Tetraphleps edacis*) in New York. Kelton (1966a, 1978) listed *Abies balsamea* L., *Pinus banksiana*, *Picea glauca*, *P. mariana*, and *Larix laricina* as host plants.

**Prey:** Drake (1921, 1922) cited the beetle, *Cryptorhynchus lapathi* Linnaeus, as prey of *Tetraphleps osborni* Drake (=*T. canadensis* Provancher), but thought that herbivorous insects on conifers, in particular *Pinus strobus*, provided most of its food. Kelton (1966, 1978) mentioned its association with the balsam woolly adelgid in eastern Canada.

**Phenology and life history:** The type of *Tetraphleps americana* Parshley (=*T. canadensis* Prov.), a female, was collected in Maine in early August and the paratype, also a female, was collected at Ottawa, Canada, in early September. Adult *Tetraphleps osborni* Drake (=*T. canadensis* Prov.) were taken in New York during July, August, and September (Drake, 1922). Drake (1922) stated that nymphs and adults were found during the summer, but the larger nymphs and adults (males and females) were found only during the latter part of the summer. He reported only a single generation per year. How this species overwinters is not known. According to Péricart (1972), adults of *T. bicuspis* (H.-S.) overwinter under the bark of their coniferous hosts. Parshley (1920) recorded no host data when he described *T. americana*.

**Distribution:** Originally described from Cape Rouge, Quebec, *Tetraphleps canadensis* Provancher is now known to occur across southern Canada from Newfoundland west to British Columbia (Kelton, 1978). Kelton (1966a) also cited Alaska, Maine, Michigan, and Wisconsin. *Tetraphleps americana* Parshley (=*T. canadensis* Provancher) was described from Maine; *T. osborni* Drake (=*T. canadensis*) from New York (Barber Point, Wanakena, and The Plains); and *T. edacis* Drake and Harris (=*T. canadensis*), from The Plains, Wanakena, New York. We report it here from coastal Oregon.

**Specimens examined:** We have examined several specimens of what appears to be this species along the Oregon coast. Oregon: Lincoln Co., Driftwood Beach Wayside, 8.5 km N Waldport, 8 August 1985, *P. c. contorta*, sample #91, 1 female.

*Tetraphleps latipennis* Van Duzee  
(Figure 10)

*Tetraphleps latipennis* Van Duzee, 1921:140; Downes, 1927:11; Harris and Shull, 1944:206; Anderson, 1958:50 (in part); Kelton and Anderson, 1962:1307; Anderson, 1962b:1331; Kelton, 1966a:201; Harris, Holms, and Dawson, 1968:15; Furniss and Carolin, 1977:81; Kelton, 1978:29; Henry, 1988:17.

*Tetraphleps profugus* Drake and Harris, 1926:42; Kelton and Anderson, 1962:1307; Kelton, 1966a:201; Henry, 1988:17.

**Diagnosis:** Length 3.50 to 4.35 mm, dorsum shiny; pubescence distinct, short and appressed. Tip of rostrum reaching anterior coxae. Pronotum with calli black, balance red brown; scutellum black; hemelytra red brown, shiny, membrane brown, narrowly pale around veins.

**Habitat:** This is a surface-feeding species, primarily a predator of small arthropods. It forages for aphids on the branches and needles of various conifers, most commonly

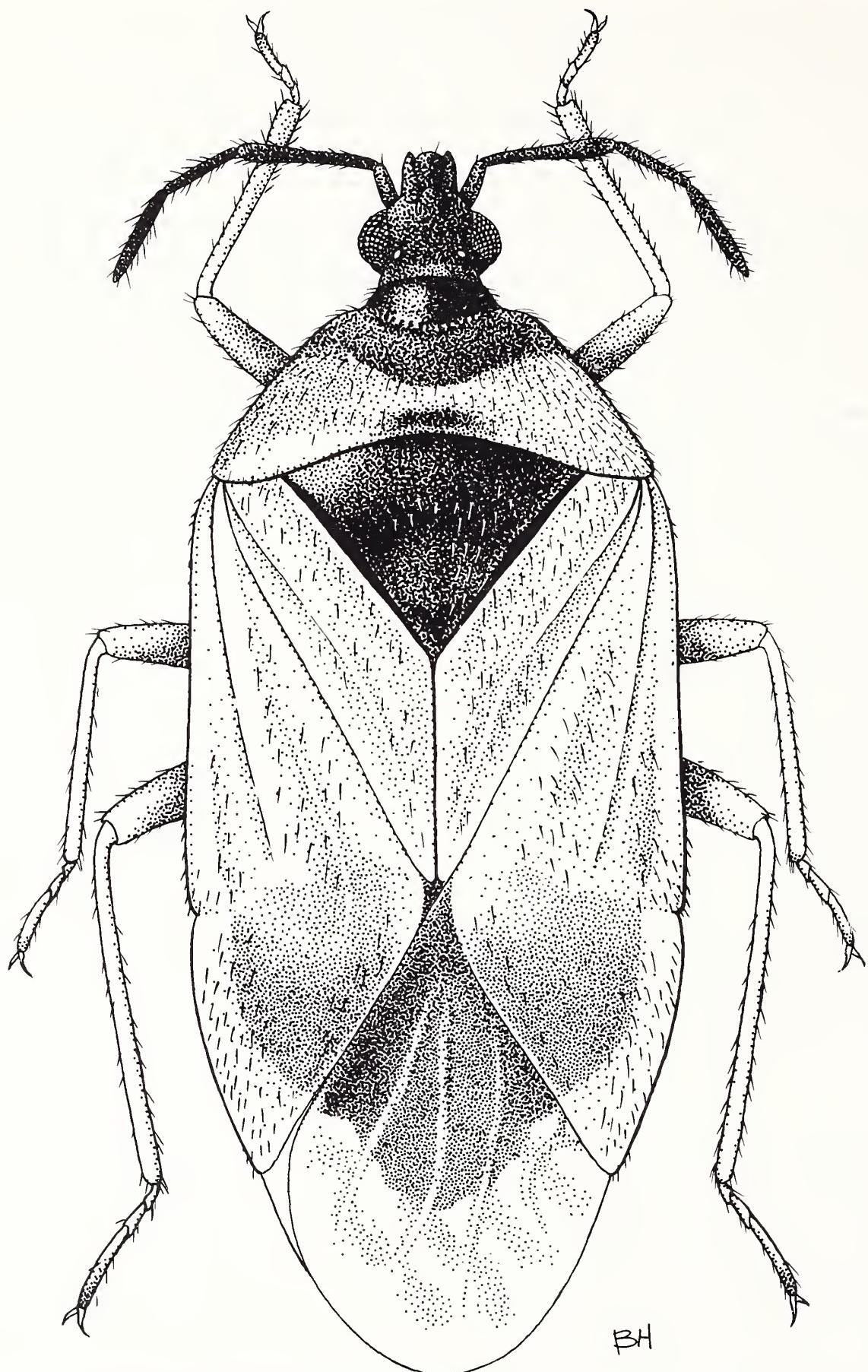


Fig. 10. *Tetraphleps latipennis* Van Duzee.

on pines. The type series was collected on white-bark pine (*P. albicaulis*) (Van Duzee, 1921); *Abies*, *Pseudotsuga*, *Picea*, *Pinus*, and *Larix* (Anderson, 1962b); *Pseudotsuga menziesii* (Mirb.); *Pinus ponderosa* Laws., *P. c. latifolia* Engelm., *Abies grandis* (Dougl.), *Picea* sp., *Larix* sp., and on *Alnus* sp. (Kelton, 1966a); *Abies grandis* (Harris, Holms, and Dawson, 1968); *Abies*, *Pseudotsuga*, *Picea*, *Pinus*, and *Larix* (Furniss and Carolin, 1977); and *Abies balsamea*, *A. amabilis*, *A. lasiocarpa*, *Larix occidentalis*, *Picea engelmanni*, *P. glauca*, *Pinus monticola*, *P. albicaulis* (Kelton, 1978). We add *P. c. murrayana* from Oregon.

**Prey:** Kelton (1966a) reported *T. latipennis* feeding on the balsam woolly adelgid in eastern Canada. Furniss and Carolin (1977) stated that this species is the most common anthocorid on conifers and reported it feeding on *Adelges cooleyi*. Kelton (1978) added "... other aphids in British Columbia."

**Phenology and life history:** Anderson (1962b) thought there were two generations per year and that the adults overwintered beginning in late August or September; the spring generation adults matured in late June or July. The only immature stages collected were fifth-instar nymphs in southeastern British Columbia in June and July together with males and females. The earliest adults in British Columbia were collected in late May and the latest, September 12. The type series, all females, were collected in California on July 28 (Van Duzee, 1921).

**Distribution:** The type series was taken on the top of Mt. Eddy (2,800 m), Siskiyou Co., California (Van Duzee, 1921). Also included in the type series were specimens from Huntington Lake (2,308 m), Fresno Co., and near Walker, Siskiyou Co., California as well as a specimen from Nanaimo, Vancouver Island, Canada. Downes (1927) reported it from Victoria, British Columbia; Harris and Shull (1944) from Moscow Mountain, Idaho; Anderson (1958) listed localities in British Columbia, Idaho, Washington; Anderson (1962b) recorded it from several other British Columbia localities, McCall, Idaho and Corvallis, Oregon. Kelton (1966a) added many localities from Alberta, British Columbia, California, New Brunswick, Newfoundland, Oregon and Wyoming; and (1978) provided a distribution map of the species in Canada. A considerable gap existed between the western and eastern localities and the map showed several localities in Saskatchewan and one in Manitoba besides the provinces already recorded.

**Specimens examined:** CANADA: British Columbia; Westbank, 12 June 1956, Douglas-fir, 1 female. UNITED STATES: California; Shasta Co., 14 km E Shasta City, 8 August 1956, *Abies shastensis*, 1 male, 2 females; Siskiyou Co., Medicine Lk. Rd., 1,846 m, 26 June 1979, *Abies concolor*, 4 females. Idaho: Benewah Co., Emida, Charlie Crk. Rd., 8 July 1979, *Abies* sp., *Abies concolor*, 4 females; Latah Co., Moscow, 25 July 1920, 1 female. Oregon: Benton Co., Mary's Peak, Saddle, 17 August 1978, Douglas-fir, 1 male, 1 female; Mary's Peak, summit, 4 October 1977, *Abies procera*, 2 females; Clackamas Co., Molalla, 1,108 m, 26 September 1977, *Abies procera*, 3 females; Deschutes Co., Three Creeks Lake, 26 km S Sisters, 2,154 m, 14 June 1990, *Pinus contorta murrayana*, 4 females; Black Butte Ranch, 13 km NW Sisters, 1,015 m, 23 March 1990, under bark of *Pinus sylvestris*, 1 female; Hood River Co., Mt. Hood, nr Silcox Hut, 2,154 m, 24 August 1980, on snow bank, 1 female; 5 km N Barlow Pass Summit, R9E T3S Sec 15 NW~, 1,372 m, 5 September 1979, *Abies amabilis*, 2 females; Jackson Co., Tubb Springs, 10 km W Pinehurst, 1,323 m, 19 May 1960, 15 females; Klamath Co., 8 km E Kirk, 1,385 m, 21 May

1958, *P. c. murrayana*, 1 female; Lake of the Woods, Rainbow Camp, 1,508 m, 23 May 1958, *Pinus c. murrayana*, 3 females; same but *Abies concolor*, 25 females; same, but *Pinus monticola*, 18 females; Lane Co., 3 km W Willamette Summit, 1,431 m, 17 July 1979, *Tsuga mertensiana*, 1 male, 1 female; Lane-Linn Co., H. J. Andrews Exp. For. R6E T15S Sec 7, SW~ 1,323 m, 31 July 1979, *Abies amabilis*, 1 male, 1 female; same but McRae Crk. crossing, FS rd 1506-359, 1,237 m, 309 August 1978, *Abies procera*, 1 female; same, 25 August 1980/860825-11 Psme-1 (*Pseudotsuga menziesii*), 1 female; Marion Co., 5 km W Breitenbush Lk., 5 June 1966, *Abies lasiocarpa*, 2 females; Multnomah Co., Portland, Black light trap, 13 August 1963, 1 male, (OSDA); Union Co., 6 km ESE Tollgate, 1,538 m, 26 June 1960, 1 female. Washington: Chelan Co., Pump Chance Crk., 4 km E Swauk Pass, 1,415 m, 10 August 1978, 1 male, 4 females; King Co., Summit, Stevens Pass, R13E T26N Sec 14, 22 August 1979, *Abies amabilis*, 5 males, 3 females; Okanagan Co., Washington Pass Mdw., 1,662 m, 11 August 1978, *Pinus albicaulis*, 1 male; Whatcom Co., Mt. Baker Nat. For., R9E T39N Sec 17, 7 September 1979, *Tsuga mertensiana*, 1 male, 1 female; Yakima Co., 5 km E White Pass Summit, 1,292 m, R12E T14N Sec 33 SW~, 22 August 1979, *Abies procera*, 5 females.

*Tetraphleps pilosipes* Kelton and Anderson

*Tetraphleps pilosipes* Kelton and Anderson, 1962:1307; Anderson, 1962b:1331; Kelton, 1966a:200; Kelton, 1978:28; Henry, 1988:17.

*Diagnosis:* Length 3.8 to 4.2 mm; head, pronotum, and scutellum black and shiny; hemelytra brown, shiny, and punctate; pubescence long and dense on pronotum, scutellum, and hemelytra. Hind tibia with long, distinct bristles. Ostiolar canal straight, slender, with narrowly rounded apex.

*Habitat:* *Tetraphleps pilosipes* is commonly beaten from the branches of its host trees. This species was originally described from specimens collected on *Abies lasiocarpa* in British Columbia and on *A. procera* in Oregon, and specimens without host data from Manitoba and the Yukon Territory (Kelton and Anderson, 1962; Anderson 1962b). Kelton (1966a) added *Larix laricina*, *Picea glauca* and *P. mariana*; he reported *Pinus albicaulis* and *P. contorta* in his 1978 paper.

*Prey:* The only positive prey information was provided by Kelton (1966a, 1978), who reported its association with the balsam woolly adelgid. Aphids of the genus *Cinara* are commonly found on *Abies procera* at the Oregon locality of Mary's Peak.

*Phenology and life history:* This species has been collected from early May to mid-October on Mary's Peak (1,231 m) near Corvallis, Oregon, and early May (British Columbia) to early September at Churchill, Manitoba. Both males and females were collected in late August at Blackwall, Manning Park, British Columbia.

*Distribution:* Described from Blackwall, Manning Park, British Columbia, the type series also contained specimens from other localities in British Columbia, Manitoba, the Yukon Territory, and Oregon (Kelton and Anderson, 1962). Records for Alaska and Newfoundland were added by Kelton (1966a) and repeated in his 1978 publication. We add records of a disjunct population in southeastern Wyoming. The occurrence of *T. pilosipes* in Newfoundland, well removed from the main area of occurrence, is perhaps paralleled by *T. latipennis* Van Duzee.

*Specimens examined:* Specimens were examined from Oregon (mainly from *Abies*

spp.), Washington, and British Columbia. We include a selection of these specimens. The record of collection from *P. contorta* given by Kelton (1978) did not give a specific locality but the distribution map shows several localities in British Columbia and the Yukon Territory that fall within the range of *P. contorta*. Specimens from Site 3.1 in Wyoming from *Pinus contorta latifolia* are reported. Colorado: Grand Co., 9 km S Fraser on Hwy 40, 17 August 1980, *Abies lasiocarpa*, 1 female. Oregon: Benton Co., Mary's Peak, nr Summit prkg. lot, 1,123 m, R7W T12S Sec 21 SW~, 2 October 1979, *Abies procera*, 2 males, 2 females; same, summit mdw., 4 October 1977, *Abies procera*, 4 males, 2 females; same, summit, 23 August 1988, *Abies procera*, 1 male, 2 females, 3 nymphs; Grass Mountain, 8 km NW Alsea, R8W T13S Sec 21 SW~, 1,092 m, 17 September 1979, *Abies procera*, 6 females; same, 985 m, 14 August 1980, *Abies procera*, 1 nymph; Clackamas Co., Molalla, 1,108 m, 26 September 1977, *Abies procera*, 4 males, 31 females; Mt. Hood, 1.5 km below Timberline Lodge, 9 September 1976, 1 male. Washington: Okanagan Co., Washington Pass Mdw., 1,662 m, 11 August 1978, 2 males, 1 female; Yakima Co., 5 km E White Pass Summit, R12E T14N Sec 33 SW~, 1,292 m, 22 August 1979, *Abies procera*, 2 females. Wyoming: Albany Co., Site 3.1, 30 July 1986, *P. c. latifolia* (trees 3, 15), 1 male, 1 female.

*Tetraphleps uniformis* Parshley

*Tetraphleps* n. sp.: Slosson, 1906:326.

*Tetraphleps uniformis* Parshley, 1920:85, Van Duzee, 1921:143; Kelton and Anderson, 1962:1307; Kelton, 1966a:202; Kelton, 1978:31; Henry, 1988:17.

*Tetraphleps furvus* Van Duzee, 1921:141; Anderson, 1958:52; Kelton and Anderson, 1962:1307; Anderson, 1962b:1331; Kelton, 1966a:202; Kelton, 1978:31; Henry, 1988:17.

*Tetraphleps concolor* Drake, 1922:68. *Nomen nudum*.

*Diagnosis:* Length 3.5 to 4.2 mm; shiny, uniformly light brown with head slightly darker and hemelytra slightly paler; pubescence dense, long. Rostrum just reaching beyond anterior coxae. Lateral margins of pronotum narrowly carinate. Membrane long, pale brown, with pale area at base end along middle of each vein. Ostiolar canal with posterior margin shallowly concave, apex broadly rounded.

*Habitat:* Little is known about the habits of this species. The original description by Parshley (1920) did not include host information, but he speculated that it would occur on conifers. Kelton (1966a) reported it from white and black spruce (*Picea glauca* and *P. mariana*), balsam fir (*Abies balsamea*) and on *Pinus contorta latifolia* and *P. sylvestris*. We add *P. c. murrayana* and *Picea engelmanni* from Oregon.

*Prey:* Kelton (1966a) stated that *T. uniformis* is associated with the balsam woolly adelgid. He repeated this prey record for eastern Canada and added that it likely feeds on other aphids on other hosts (1978). This anthocorid was very abundant on several *P. c. murrayana* heavily infested with a species of *Cinara* near Sisters, Oregon. *Melancoris nigricornis*, another anthocorid, was taken in lesser numbers from the same trees.

*Phenology and life history:* Although locality records of this species have been published (Parshley, 1920; Kelton, 1966a), no collecting dates were included. The specimens we have examined bore dates ranging from May to September.

*Distribution:* Parshley (1920) described this species from a female collected on Mt. Washington, New Hampshire. Kelton (1966a) added many localities from Newfoundland west to British Columbia and the Yukon Territory in Canada and added Maine, New York, and Colorado in the United States. He also gave a map showing transcontinental distribution in Canada.

We saw some distinct differences in specimens from the Rocky Mountains of Wyoming and Colorado, especially in the shape and length of the pronotum, and length of the membrane. The color pattern of the typical specimen, rather uniformly brown, differs considerably from those of Kelton (1966) (head, pronotum and scutellum black). We have examined specimens from Colorado and Wyoming that fit the description of *T. furvus* very well. Careful study of specimens from throughout the range is likely to disclose more than a single species.

*Specimens examined:* Colorado: Grand Co., 8.6 km S Fraser on Hwy 40, 17 August 1980, *P. contorta latifolia*, 1 female; Gilpin Co., 3 km S Guanella Pass 3,015 m, 4 September 1991, *P. c. latifolia*, 1 female, 1 male. Oregon: Deschutes Co., Site 8, 20 August 1986, *Picea engelmanni* (10 pooled trees), 1 female; Site 10, 10 June 1986, *Abies lasiocarpa*, 1 female; Three Creeks Lake, 26 km S Sisters, 2,069 m, 14 June 1990, *P. c. murrayana*, 8 females; 7 October 1989, *P. c. murrayana*, 2 females. Wyoming: Albany Co., Site 3.1, 11 July 1986, *P. c. latifolia* (tree 19), 1 female; Site 3.1, 30 July 1986, *P. c. latifolia* (trees 3, 13, 15, 16), 5 males, 2 females; Carbon Co., Site 4.1, 17 July 1986, *P. c. latifolia* (tree 2), 1 male; Site 4.2, 11 July 1986, *P. c. latifolia* (tree 19), 2 females; Site 4.2, 12 July 1986, *P. c. latifolia* (tree 10), I-V instar nymph, Site 4.2, 17 July 1986, *P. c. latifolia* (trees 6, 11), 2 females.

### *Xylocoris* Dufour

*Xylocoris* Dufour, 1831:423; Van Duzee, 1917a:290; Chu, 1969:47; Carayon, 1972a: 337; 1972b:579; Péricart, 1972:210; Herring, 1976:70; Kelton, 1976a:193; Kerzhner and Elov, 1976:364; Kelton, 1977b:1017; Kelton, 1978:63; Kerzhner, 1988: 771; Henry, 1988:26.

*Diagnosis:* Small, smooth, shiny species; both sexes may be macropterous or brachypterous. Antennal segments one and two of normal thickness, segments three and four slender, with long setae. Pronotum shiny, collar narrow, lateral margins carinate. Hemelytra punctate or smooth, with or without pubescence; membrane, when present, with four veins. Metacoxae proximate; ostiolar canal well developed, curved or angled. Males with anterior and middle tibiae with pads. Left clasper only; ovipositor well developed.

The genus *Xylocoris* contains approximately 30 described species. Although widely distributed in the world, most of the species are found in the northern temperate regions (Chu, 1969; Carayon, 1972a, b; Péricart, 1972). The type of the genus is *Xylocoris rufipennis* Dufour, a junior synonym of *Lygaeus cursitans* Fallén. Chu (1969) presented a list of world species. The genus contains four subgenera (Carayon, 1972b; Péricart, 1972). Representatives of three of the four subgenera occur in North America and twelve species are known in America north of Mexico (Henry, 1988). Three of these, including *X. cursitans*, are considered introductions into the Nearctic (Kelton, 1978; Henry, 1988).

Species of *Xylocoris* occur in quite different habitats, ranging from leaf litter, stored-

grain facilities, to subcorticular environments, sometimes entering the galleries of bark beetles (Trägardh, 1914; Sands, 1957; Southwood and Leston, 1959; Anderson, 1962b; Péricart, 1972; Kelton, 1978). Aside from the several species known to occur in stored grain, little is known about the habits of the North American *Xylocoris*. Chu (1969) provided a detailed study of *X. galactinus* (Fieber) in Japan. Papers by Arbogast (1979) and Arbogast, Flaherty, and Press (1983) provided similar information on *X. flavipes* (Reuter) and *X. sordidus* (Reuter), respectively, in North America.

The North American fauna needs careful study to clarify the status of almost all of the species, including those considered to be introductions. Because of the low vagility of brachypterous forms, for example, it is difficult to imagine their rapid dispersal in natural forests. At present, no key exists for the North American species. Kelton (1976a, 1978) provided descriptions of several species and a key to the four species found in Canada and Alaska. Chu (1969), Carayon (1972b), Péricart (1972), Kerzhner and Elov (1976), and Kerzhner (1988) provide valuable information on the Palearctic fauna.

*Xylocoris californicus* (Reuter)

*Piezostethus californicus* Reuter, 1884:600; Lethierry and Severin, 1896:239; Van Duzee, 1917a:291.

*Xylocoris californicus*: Van Duzee, 1916:34; 1917a:291; 1921:138; Harris and Shull, 1944:207; Anderson, 1962b:1326; Chu, 1969:18.

*Xylocoris (Xylocoris) californicus*: Henry, 1988:27.

**Diagnosis:** Macropterous. Length 3 mm. Dark brown to black, smooth, shiny. Apex of rostrum attaining middle coxae. Pronotum polished, calli indistinct, transverse impression absent. Hemelytron largely pale with inner margin of clavus and commissural margin piceus, also apex of embolium and all of cuneus except inner angle, piceus. Ostiolar canal curved, apex obtuse, ending some distance from anterior margin of metapleuron; area anterior to canal, broad and striate.

*Xylocoris californicus* is similar to *X. umbrinus* Van Duzee. It may be separated from the latter by the paler portions of the hemelytra (*X. umbrinus* tends to be largely brown to dark brown), and the shorter ostiolar canal with more of the evaporative area anterior to the canal than in *X. umbrinus*, where the canal is longer and approaches the anterior edge of the metapleuron. Van Duzee (1921) compared the two species.

**Habitat:** Little is known about the habitat of this species. The female reported here was collected from the branches of *P. c. murrayana* near Bartle, California. Since this species appears close to *X. umbrinus* Van Duzee, it is possible that some of the records for *X. californicus* actually refer to *X. umbrinus*. Van Duzee (1921) reported taking *X. californicus* at Cayton and Bryson, California, the same localities as the type series of *X. umbrinus*. He mentioned a female of *X. umbrinus* taken at Cayton under the bark of an old fir log. The only host plant information available is that of *Pinus contorta murrayana* from the specimen taken near Bartle, Siskiyou Co., California.

**Prey:** No information is available regarding the specific prey of this species.

**Phenology and life history:** Harris and Shull (1944) reported collections from July

14 to September 19 in Idaho. The female we report here was collected in late June in northern California. No information is available about its life history.

*Distribution:* *Xylocoris californicus* was originally described from Mariposa, Mariposa Co., California (as *Piezostethus californicus*) (Reuter, 1884). Van Duzee reported it from Utah, New Mexico and California (1917a) and from Cayton, Shasta Co., and Bryson, Monterey Co., California (1921). Harris and Shull (1944) reported the species from Hagerman and Twin Falls, Idaho. Anderson (1962b) added Merrill and Klamath Falls, Oregon.

*Specimens examined:* California: Siskiyou Co., 2 km E Bartle, Hwy. 89, 1,246 m, 21 June 1981, *P. c. murrayana*, 1 macropterous female.

*Xylocoris cursitans* (Fallén)  
(Figure 11)

*Lygaeus cursitans* Fallén, 1807:74.

*Piezostethus cursitans*: Reuter, 1871:411; 1884:43; Van Duzee, 1914:14.

*Xylocoris cursitans*: Van Duzee, 1916:34; 1917a:291; 1921:137; Harris and Shull, 1944:207; Sands, 1957:305; Southwood and Leston, 1959:185; Anderson, 1962b: 1326; Carayon, 1972b:582, 593; Péricart, 1972:228; Kelton, 1978:68; Henry, 1988:27.

*Xylocoris vicarius*: Anderson, 1962b:1326.

*Diagnosis:* Length 1.8–2.5 mm, width 0.70–1 mm, dark red brown to black, shiny, smooth. Tip of rostrum reaching middle of mesosternum. Pronotum black, shiny, calli smooth, basal portion transversely rugose. Scutellum with basal portion smooth, apical portion rugose, a slightly elevated median carina. Hemelytra (macropterous form) smooth, shiny, with moderately long, semi-erect and dense golden pubescence; corium and clavus adjacent to corium pale, balance of wing dark brown to black; membrane pruinose, only outer vein distinct. Hemelytra of brachypterous form reduced, extending to posterior margin of abdominal segment three; membrane greatly reduced. Ostiolar canal strongly bowed. Male clasper slender and sinuate.

*Habitat:* The principal habitat is beneath the bark of dead trees, both deciduous and coniferous (Trägårdh, 1914; Sands, 1957; Southwood and Leston, 1959; Anderson 1962b; Péricart, 1972; and Kelton, 1978). Rarely it has been found in granaries, leaf litter, and on plants (only macropterous forms in the latter) (Sands, 1957; Péricart, 1972). It seems most abundant under bark of trees in the early stages of decay (Southwood and Leston, 1959). Such genera as *Quercus*, *Fagus*, *Fraxinus* and *Populus* have been cited as examples of deciduous trees, while *Pinus* has been reported as the coniferous example (Sands, 1957; Anderson, 1962b; Péricart, 1972). We report its occurrence here under the bark of *P. c. contorta*.

*Prey:* Anderson (1962b) cited its association with dipterous larvae (likely Mycetophilidae) under bark. He was able to rear it on aphids in the laboratory. Morkrzecki (1923) reported this species feeding on *Ips typographus* Linnaeus. Péricart (1972) suggested a variety of prey, such as the larvae of many insects and other subcorticular arthropods including larval Scolytidae, other beetles, thrips, and Collembola.

*Phenology and life history:* Anderson (1962b) reported that the number of generations per year had not been established although most life stages were present throughout most of the year. Both nymphs and adults overwinter under the bark of

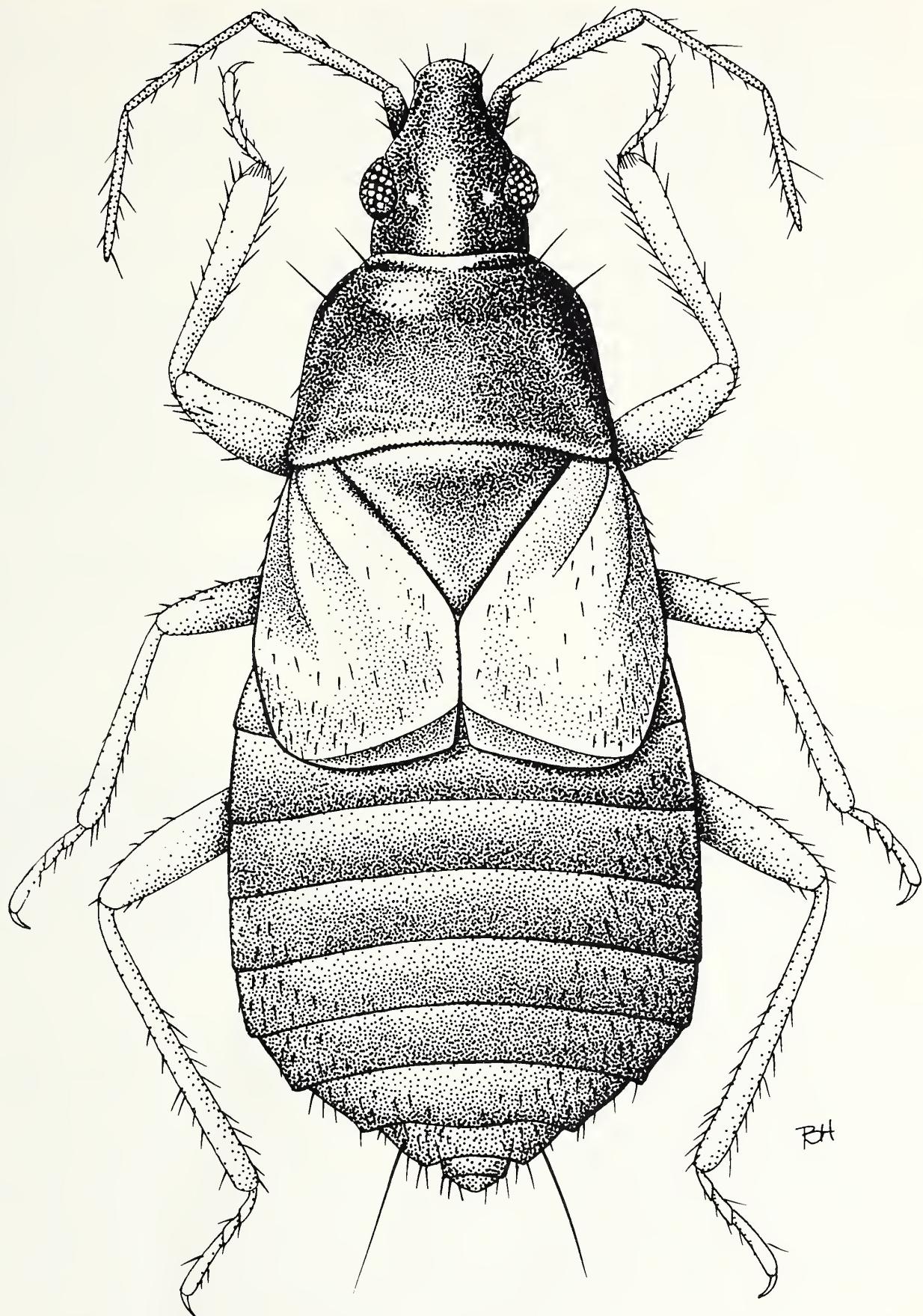


Fig. 11. *Xylocoris cursitans* (Fallén).

trees, although true diapause appears to be lacking (Péricart, 1972). Péricart (1972) suggested at least two or three generations occur per year. The eggs are deposited on the inner surface of the bark or rotten wood (Anderson, 1962b). The same author reported that the eggs hatched in 8 to 10 days. The nymphs develop slowly, even under laboratory conditions, requiring from 58 to 62 days to reach the adult stage. He reported that adults were long lived, one living for 80 days. This long adult life could account for the overlap between generations.

**Distribution:** *Xylocoris cursitans* is a Palearctic species, originally described from Sweden. It is considered to be an introduction into North America, first recorded by Van Duzee (1916). According to Henry (1988), it has been reported from Alberta, British Columbia, Connecticut, Idaho, Indiana, Michigan, New Jersey, Nova Scotia, New York, Ontario, Oregon, and Quebec. To these records, we add Washington. Within the range of *P. contorta*, the species is known from southern British Columbia and Alberta, south into Idaho, western Washington, through western Oregon (Anderson, 1962b). Some of these localities are well removed from areas where introductions might be considered reasonable, especially since this species does not appear to be particularly vagile.

**Specimens examined:** Washington: Kitsap Co., Bremerton, 2 November 1974, under bark of *Pinus contorta* killed in 1972; abandoned by Scolytidae, 1 macropterous female, 1 brachypterous female.

#### DISCUSSION

##### HOST PLANT ASSOCIATION

Although the Anthocoridae are primarily predaceous, some show remarkable fidelity to particular plants at various taxonomic levels (i.e., conifers or a particular genus of plants). Of the 28 genera of Anthocoridae known from Canada and the United States, 8 have some or all of their species occurring on conifers and two (*Anthocoris* and *Orius*) are occasionally found on conifers, although they live chiefly on broad-leaved plants. Five of the eight genera (*Acompocoris*, *Elatophilus*, *Melanocoris*, *Tetraphleps*, and *Scoloposcelis*) occur only on conifers. *Cardiastethus*, *Lycotocoris*, and *Xylocoris* occur on non-coniferous trees as well.

All of the species reported in this paper were taken on conifers (Table 2), although two of the genera (*Anthocoris* and *Orius*) should be regarded more as casual visitors from broad-leaved plants. They are, however, broadly foraging predators and do become involved with insects on *Pinus contorta* (Reid, 1957). Species of several of the genera (*Acompocoris*, *Elatophilus*, *Melanocoris*, *Cardiastethus*, *Scoloposcelis*, and *Xylocoris*) occur chiefly on species of *Pinus*. Ten species have been taken on several species of *Picea*, six species on several species of *Abies*, four species on species of *Larix*, and two species on *Pseudotsuga*. The diversity of coniferous hosts in western North America certainly contributes to the diversity of the Anthocoridae found on them. All of these hosts are in the Pinaceae; none has been taken from plants of the family Cupressaceae. Specimens of *Dufouriella ater* (Dufour) were taken from *Juniperus occidentalis* near Sisters, Oregon, but this species was not taken from *Pinus contorta murrayana* or *P. ponderosa* occurring in the immediate vicinity. Several of the taxa, notably *Melanocoris longirostris*, all five species of *Tetraphleps*, and *Scoloposcelis flavicornis*, show wide host plant associations. How many of these represent

Table 2. Occurrence of Anthocoridae on different subspecies of *Pinus contorta*.

	<i>Pinus contorta contorta</i>	<i>Pinus contorta murrayana</i>	<i>Pinus contorta latifolia</i>
<i>Acomporocoris lepidus</i>		OR	BC, YT, COLO, WY
<i>Anthocoris antevolens</i>	BC		ALB
<i>Anthocoris musculus</i>			
<i>Elatophilus dimidiatus</i>		CA, OR	
<i>Elatophilus pullus</i>	WA		WY
<i>Elatophilus</i> sp. A		CA, OR	
<i>Melanocoris longirostris</i>		CA, OR	COLO, WY
<i>Melanocoris nigricornis</i>		CA, OR, MEX	BC, WY
<i>Tetraphleps canadensis</i>	OR		
<i>Tetraphleps latipennis</i>		OR	BC
<i>Tetraphleps pilosipes</i>			BC, WY
<i>Tetraphleps uniformis</i>		OR	COLO, WY
<i>Orius tristicolor</i>		OR, MEX	
<i>Cardiastethus borealis</i>			OR
<i>Lyctocoris tuberosus</i>		OR	BC
<i>Scoloposcelis flavigornis</i>	WA	OR	MT
<i>Xylocoris californicus</i>		CA	
<i>Xylocoris cursitans</i>	WA		

hosts upon which the insects breed rather than "sitting" records remains to be determined. The capability to identify immature individuals to species would be of great value. It does appear that greater host plant breadth occurs in the northern regions (i.e., Canada and northern United States) but that may be an artifact of collecting or the dominance of conifers over broad-leaved trees in the same area. Again, close attention to the occurrence of immature stages should clarify this matter.

#### FEEDING HABITS

The Anthocoridae are generally regarded as predaceous, although there is ample evidence that some plant feeding occurs in some species (e.g., Dicke and Jarvis, 1962; Chu, 1969; Bachelor and Baranowski, 1975). Members of this family are part of the guild of predators found on a variety of plants (Carayon, 1961; Anderson, 1962b; Péricart, 1972; Evans, 1976a, b, c, d), but detailed biological studies have been confined largely to species occurring in agroecosystems (e.g., Collyer, 1953; Sands, 1957; Carayon, 1961; Anderson, 1962a, b; Chu, 1969; Evans, 1976a, b, c, d; Ryerson and Stone, 1979; Arbogast, 1979, 1984). Some predaceous species have been introduced as biological control agents (e.g., Davis and Krauss, 1963; Mitchell and Wright, 1967; Harris, Holms, and Dawson, 1968).

Less information is available on the genera and species found on conifers, and much of it is contained in taxonomic papers or those dealing with collections of insects from different localities or from different hosts. Some have well-defined feeding habits that suggest prey specificity, a phenomenon also noticed in some other insect predators (Thompson, 1951).

### Generalist Feeders

The genus *Anthocoris* contains many species that feed on a variety of prey, usually scaled to their size (Carayon, 1961; Evans, 1976a). They forage over the surface of trees, and, to a lesser extent, shrubs for aphids, scales, young lepidopterous larvae, thrips, mites, and other small arthropods. *Orius* contains several very small species that occur on many different plants, including a variety of forbs and grasses. Both genera are normally found on deciduous plants but *Anthocoris antevolans* and *A. musculus*, and *Orius tristicolor* were taken on *Pinus contorta* (Evans, 1983; Reid, 1957; this study). The genus *Tetraphleps* is a coniferous analogue of *Anthocoris*, but it seems more specific in its feeding habits—chiefly Homoptera, and especially aphids (Péricart, 1972).

*Lyctocoris beneficus* (Hiura), a species similar to *L. campestris*, occurs in Japan and Korea (Chu, 1969). Chu (1969) provided a detailed study of this species and *Xylocoris galactinus* (Fieber). While both species were primarily predaceous, they were able to survive for short periods feeding on moldy grain. Reproduction did not occur when restricted to such food.

### Specialist Feeders

**Aphids:** Anthocorids that feed on aphids are surface dwellers. This group contains the generalist feeders (*Anthocoris* and *Orius*); but it also contains three genera (*Acompocoris*, *Melanocoris*, and *Tetraphleps*) that appear to feed chiefly upon aphids. According to Péricart (1972), *Acompocoris pygmaeus* feeds on *Cinara pinicola* Kaltenbach and *Schizolachnus pineti* Fabricius in Europe. *Acompocoris lepidus* occurs on *Pinus contorta murrayana* in North America, together with the aphids *Cinara* spp. and *Essigella* spp. Foottit and Mackauer (1990) provide information on populations of *Cinara nigra* (Wilson), a widely distributed species found on *Pinus contorta*.

*Melanocoris nigricornis* has been taken in association with the aphids *Cinara* sp., *Essigella fusca* and the pine needle scale, *Phenacaspis pinifoliae* (Anderson, 1962b). Both genera of aphids were taken in our collections.

The balsam woolly adelgid, *Adelges piceae*, is a major pest of the true firs (*Abies* spp.) in boreal North America. A native of Europe, it was first recorded from North America in 1908 from Maine (Drooz, 1985). Today, it occurs in the eastern and far western parts of Canada and the United States (Furniss and Carolin, 1977; Foottit and Mackauer, 1983). *Acompocoris lepidus* is reported to feed on this insect in the central Cascade Mountains of Oregon (Mitchell, 1962). Several native species of *Tetraphleps* have been reported occurring with the aphid, including *T. canadensis* (Kelton, 1966a, 1978), *T. latipennis* (Kelton, 1966a, 1978; Harris, Holms, and Dawson, 1968; Furniss and Carolin, 1977), and *T. uniformis* (Kelton, 1966a, 1978).

**Bark beetles:** A number of genera and species of Anthocoridae are found associated with bark beetles (Coleoptera: Scolytidae). These bugs are generally found in the galleries where they feed upon the eggs and larvae of the beetles.

Although not usually regarded as a conifer inhabitant, *Anthocoris musculus* (Say) has been recorded as an egg predator of *Ips* bark beetles on lodgepole pine by Reid (1957). Kline and Rudinsky (1964), Furniss and Carolin (1977), and Dahlsten (1982) reported *Lyctocoris* sp. or spp. from bark beetle galleries. Fronk (1947) reported *L. elongatus* (Reuter) as a predator of the southern pine beetle, *Dendroctonus frontalis*

Zimmerman, as did Dixon and Payne (1979), Mosier, Thatcher, and Pickard (1971), Berisford (1980), and Goyer, Lenhart, Nebeker, and Schmitt (1985). Moore (1972) and Berisford (1980) also recorded *L. campestris* (F.) feeding on the same beetle. Kelton (1967) reported *L. tuberosus* Kelton and Anderson as an associate of *Ips* spp. found on several hosts, including *P. contorta*. He (Kelton, 1967) also reported *L. mexicanus* Kelton in association with the bark beetles *Ips* and *Dendroctonus* spp., the weevils *Cossinus* spp., and the buprestids *Chrysobothris* spp.

Carayon (1953a) provided a detailed study of *Scoloposcelis obscurella* (Zett.) in France, where the bug feeds upon the larvae of several species of Scolytidae. In North America, Drake (1922) reported *Scoloposcelis flavidicornis* Reuter (as *Anthocoris* sp.) from the galleries of a number of bark and ambrosia beetles in New York. Drake and Harris (1926) described several species of *Scoloposcelis*, including *S. mississippiensis*, taken from the burrows of bark beetles on long-leaf pine. Mosier, Thatcher, and Pickard (1971) reported this species as an associate of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, as did Moore (1972), Dixon and Payne (1979), Berisford (1980) and Goyer, Lenhart, Nebeker, and Schmitt (1985). Dahlsten (1970) recorded a species of *Scoloposcelis* (likely *S. flavidicornis*) from *Pinus ponderosa* bark disks infested with *Dendroctonus brevicomis* LeConte. Ohmart (1981) reported *S. flavidicornis* from the foliage of *Pinus radiata* D. Don, and from the brood galleries of *Ips paracanfusus* Lanier. Dahlsten (1982) found *Scoloposcelis* spp. common in adult and egg galleries of bark beetles. He pointed out the problems predators face in coping with the clumped distribution of their prey and that they may locate them by chance encounters; however, Borden (1982), citing Dixon and Payne (1979), reported a species of *Scoloposcelis* that was attracted to the aggregation pheromones of Scolytidae.

*Xylocoris cursitans* (Fallén) is common under bark. According to Chu (1969), Trägårdh (1914) was the first to report it as a predator of bark beetle larvae. He also cited Morkrzecki's (1923) record of *X. cursitans* feeding on *Ips typographus* Linnaeus in Europe.

*Bark-lice:* *Cardiastethus fasciiventris* (Gariglietti), a European species, is reported to feed on Psocoptera (Péricart, 1972), but no specific prey data have been given for *C. borealis* Kelton, our only North American species found on conifers. *Cardiastethus borealis* has been found on *Pinus ponderosa*, *P. banksiana*, and *P. sylvestris* (Kelton, 1978) and report it here on *P. contorta latifolia* in central Oregon. Psocoptera are usually abundant on most of these species of pines, and thus, potentially available as prey.

*Mites:* In Europe, *Brachysteles parvicornis* (Costa), reported recently from North America by Asquith and Lattin (1990), feeds on members of the mite suborder Oribatida in Europe (Carayon, cited in Péricart, 1972). Specimens were collected in Maine and Massachusetts, on *Picea glauca* (Moench) Voss and *Pinus rigida* Miller, in association with the cosmopolitan oribatid *Humerobates rostrolamellatus* Grandjean (Family Ceratozetidae) (Lattin and Asquith, 1991).

*Needle miners:* Struble (1967) reported occasional predation on the lodgepole needle miner, *Coleotechnites milleri* (Busck) (Lepidoptera: Gelechiidae) on *Pinus contorta murrayana* by an unidentified species of Anthocoridae in Yosemite National Park, California.

*Scale insects:* Anderson (1958) associated *Elatophilus pullus* (as *Elatophilus* sp. b.)

and *Melanocoris nigricornis* (Anderson, 1962b) with the pine needle scale, *Chionapis (Phenacaspis) pinifoliae*. Species of the genus *Elatophilus* feed primarily on various Coccoidea, chiefly species of the scale genus *Matsucoccus* (Homoptera: Magarodidae) (Biliotti and Riom, 1967; Cobben and Arnaud, 1969; Drooz, 1985; Mendel, Carmi, and Podoler, 1991). Lussier (1965) provided a detailed study of *Elatophilus inimica* preying on red pine scale, *Matsucoccus resinosae*. Although there is at least one species of *Matsucoccus* and several species of *Elatophilus* on lodgepole pine, no direct feeding observations have yet been made.

*Subcorticular insects:* The flattened shape of Anthocoridae makes them well adapted for preying on insects under bark (Hamilton, 1978). Some species of *Elatophilus* are known to feed on scales in the genus *Matsucoccus* (Lussier, 1965; Mendel, Carmi and Podoler, 1991). *Lyctocoris campestris* (F.) has been taken under bark (Anderson, 1962b), as have other species of *Lyctocoris* (e.g., Kelton, 1967; Goyer, Lenhart, Nebeker, and Schmitt, 1985). *Scoloposcelis flavigornis* Reuter is a subcorticular species that also enters bark beetle burrows (e.g., Drake, 1922; Mosier, Thatcher, and Pickart, 1971; Goyer, Lenhart, Nebeker, and Schmitt, 1985). *Xylocoris cursitans* is commonly collected under the bark of dead trees (e.g., Trägardh, 1914; Anderson, 1962b; Péricart, 1972; Kelton, 1978). One from the type series of *Xylocoris umbrinus* was collected under the bark of an old fir log (Van Duzee, 1921). Many other species of *Xylocoris* are found in leaf litter (e.g., Anderson, 1962b; Carayon, 1972b; Péricart, 1972; Kerzhner and Elov, 1976; Kelton, 1976a).

## INTRODUCTIONS

At least twelve species of Anthocoridae have been introduced into North America either accidentally [(e.g., *Acomporis pygmaeus* (Fallén), *Brachysteles parvicornis* (Costa), and *Orius minutus* (Linneaus)] or deliberately [e.g., *Anthocoris nemoralis* (Fabricius)]; none has yet been taken on *Pinus contorta* (Anderson, 1962b; McMullen and Jong, 1967; Kelton, 1978; Henry, 1988; Lattin, Asquith, and Booth, 1989; Asquith and Lattin, 1990; Lattin and Asquith, 1991). At least four species are conifer associates (e.g., *Acomporis pygmaeus*, two species of *Tetraphleps* and *Brachysteles parvicornis*), while the others are found on broad-leaved hosts, in litter, or in stored-grain facilities. *Tetraphleps abdulghanii* Ghauri and *T. raoi* Ghauri have been introduced into North America from Pakistan and India, respectively, as predators of the balsam woolly adelgid, a pest of true firs (Ghauri, 1964; Mitchell and Wright, 1967; Harris, Holms and Dawson, 1968), but apparently they have not become established (L. M. Humble and R. G. Mitchell, pers. comm., March, 1990). *Xylocoris cursitans* (Fallén), found on *P. contorta*, may be naturally Holarctic, rather than an introduction; it occupies essentially the same habitat in both hemispheres—the galleries of beetles, usually Scolytidae, beneath the bark of both coniferous and deciduous trees. *Xylocoris galactinus* (Fieber), found chiefly in organic litter and stored grain, sometimes under bark, may be an introduction rather than a naturally Holarctic species.

Two species, *A. confusus* Reuter and *A. nemoralis* (Fabricius), have been introduced accidentally from Europe. The latter species subsequently was introduced into southern British Columbia from Switzerland in 1963 as a potential biological control agent for the pear psylla (McMullen and Jong, 1967; McMullen, 1971; Fields and Beirne, 1973). This species seems to have adapted to orchards in the Pacific Northwest.

Much less is known about *A. confusus*, but its range has been expanding (Kelton, 1978; Scudder, 1986).

#### WING POLYMORPHISM

In the Anthocoridae wing reduction is usually correlated with cryptic habits; under and within cracks and crevices of bark; and, to a lesser extent, within the litter layer. Wing reduction, either by brachyptery or microptery, occurs in a number of genera of Anthocoridae (Péricart, 1972; Kelton, 1978), including several collected during this study (*Anthocoris*, *Elatophilus*, and *Xylocoris*). Brachyptery is more common than microptery (Péricart, 1972). While wing modification may occur in both sexes, it is most common in females. Psocoptera show a similar trend (Thornton, 1985).

Hamilton (1978) considered the subcorticular habitat to have been of considerable evolutionary importance in the insects. He included examples of several genera of Anthocoridae (*Xylocoris* and *Anthocoris*) in his discussions; representatives of both of these genera have been collected from *P. contorta*.

The reduction of wing size and development, accompanied by the loss of flight, is often associated with some degree of habitat stability (Usinger, 1950; Southwood, 1961, 1962; Hamilton and May, 1977; Slater, 1977; Hamilton, 1978; Denno and Grissell, 1979; Greenwood, 1988; Roff, 1990). Insects with reduced wings, or lacking wings entirely, are found frequently on large bodies of water, including the oceans (e.g., *Halobates*), in the ground or in the litter layer, as ectoparasites, and under bark. In contrast, insects with high flight activity are normally associated with temporary habitats (Southwood, 1960).

Wing reduction in the Heteroptera sometimes results in fewer nymphal instars during development. Stys and Davidova-Vilímová (1989) reviewed unusual numbers of instars in the Heteroptera and, citing Péricart (1972) for *Temnostethus gracilis* Horváth, suggested that Anthocoridae displaying wing reduction may have a reduced number of developmental stages.

We collected three brachypterous females of *Elatophilus dimidiatus* (Van Duzee) from the branches of *P. contorta murrayana* outside of Lassen National Park in Tehama Co., California. Another series of specimens was collected above Big Bear Lake, San Bernardino Co., California, on the same host; the four males were macropterous and the 12 females were brachypterous. We also collected a brachypterous male and brachypterous females of an undescribed species of *Elatophilus* from *Pinus ponderosa* near Sisters, Oregon. The genus *Elatophilus* had been regarded as always macropterous (Péricart, 1972; Kelton, 1976b, 1978), but see our discussion under *E. dimidiatus*. A brachypterous female of *Xylocoris cursitans* (Fallén) was taken under the bark of *P. c. contorta* killed by Scolytidae at Bremerton, Washington; a macropterous female was collected at the same time. Kelton (1978) found *X. cursitans* in Canada under the bark of dead trees, both coniferous and deciduous. Both sexes occur in the macropterous and brachypterous state in Europe and North America. Two additional species, *X. galactinus* (Fieber) and *X. umbrinus* (Van Duzee), are known to occur under the bark of trees in North America, but neither has yet been collected from *P. contorta*. *Xylocoris galactinus* is only known in the macropterous state, while both sexes of *X. umbrinus* occur in the macropterous and brachypterous state.

It is interesting that brachypterous males and females have ocelli. Many taxa in the Heteroptera lose their ocelli when the wings are reduced (e.g., Lygaeidae). According to Péricart (1972), brachypterous females in the family Microphysidae lack ocelli, or else they are vestigial, and the strongly brachypterous Cimicidae lack ocelli in both sexes. However, Pericart (1972) reported that the brachypterous *Xylocoris thomsoni* (Reuter) was the only brachypterous anthocorid lacking ocelli known from the western Palearctic Region.

#### RESEARCH NEEDS

This is an interesting family of insects about which we know relatively little. Most species are predators of small insects and other arthropods, including such pests as the balsam woolly adelgid, some scale insects and bark beetles. The various genera and species often show specific host plant and habitat preference, the details of which are largely unknown. Biological and ecological studies of most species would be useful. Our knowledge of the distribution of nearly all species is fragmentary at best with much additional collecting needed. Generic revisions are needed to allow accurate identification of the various taxa, including consideration of species variation throughout their range. Sands (1957), Anderson (1958), and Péricart (1972) have shown that eggs and nymphs can be recognized, often to species, thus encouraging further work with these stages. Finally, a well-illustrated and updated key to the genera of the Anthocoridae of North America would be of value.

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**SEASONAL OCCURRENCE OF THE MIRIDAE  
(HETEROPTERA) ASSOCIATED WITH OHIO BUCKEYE,  
*AESCULUS GLABRA* WILLD., IN MISSOURI**

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*Abstract.*—Seasonal history of the mirids *Lygocoris aesculi* (Knight), *Microphylellus modestus* Reuter, and *Orthotylus aesculicola* Blinn was followed on *Aesculus glabra* Willd. in central Missouri during 1985–86. The activity period of these univoltine plant bugs was confined to late March to early June, concurrent with the onset of flowering and leaf flush, with almost complete overlap between the species. The adult male of *L. aesculi* and the fifth-instar nymphs of all 3 species are described and illustrated.

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The large plant bug genera *Lygocoris* Reuter and *Orthotylus* Fieber are better known compared to many other mirid genera, with respect to their host plants and distribution; much less is known about the genus *Microphylellus* Reuter. Members of these genera are in general arboreal and feed on a variety of trees and shrubs. Ohio buckeye, *Aesculus glabra* Willd., is interesting because it is a host of 1 species each of *Lygocoris* and *Orthotylus*, both of which are known only from Missouri. The discovery in 1984 of breeding populations of these little-known plant bugs, *Lygocoris aesculi* (Knight), and *Orthotylus aesculicola* Blinn, and the more widely known *Microphylellus modestus* Reuter, was the motivation for this study.

Herein I summarize the distribution, seasonal occurrence, and food habits for the 3 mirids found breeding on Ohio buckeye in Missouri. Descriptions of the adult male of *L. aesculi* (Knight) and of the fifth instars of the 3 species are also given.

**STUDY SITE AND METHODS**

The study site in Columbia (Boone Co.), Missouri, was a rocky, southern-exposed slope in a wooded area dominated by white oak, *Quercus alba* L., and shagbark hickory, *Carya ovata* (Mill.) K. Koch, with an understory of mostly Ohio buckeye, *A. glabra* Willd., and serviceberry, *Amelanchier arborea* (Michx. f.) Fern. The buckeyes were a mixture of mature and young trees ranging from 2–10 meters high.

Sampling began at, or slightly before, bud break to determine earliest eclosion (9 April in 1985; 31 March in 1986) and continued every 3 to 7 days until adults were no longer collected (early June). Mirids were sampled visually by inspecting the foliage and flowers of Ohio buckeye trees for ca. 30 minutes, and any specimens observed were captured. If an adequate sample was not obtained by visual inspection, the branches were shaken into a standard 15-inch beating net to obtain additional specimens. The numbers were generally small, with a typical sample consisting of 10 or fewer specimens of each species. Immatures were placed in alcohol and sorted to species and instar in the laboratory; preserved adults and immatures were deposited

as voucher specimens in the North Carolina State University Insect Collection, Raleigh. All measurements are in millimeters.

#### RESULTS AND DISCUSSION

##### *Lygocoris aesculi* (Knight)

Known only from Missouri, this mirine was originally described by Knight (1953) as *Neolygus aesculi* from three females collected on "buckeye leaves" in Kansas City (Jackson Co.). Blinn and Yonke (1985) collected this species in Columbia (Boone Co.) on Ohio buckeye.

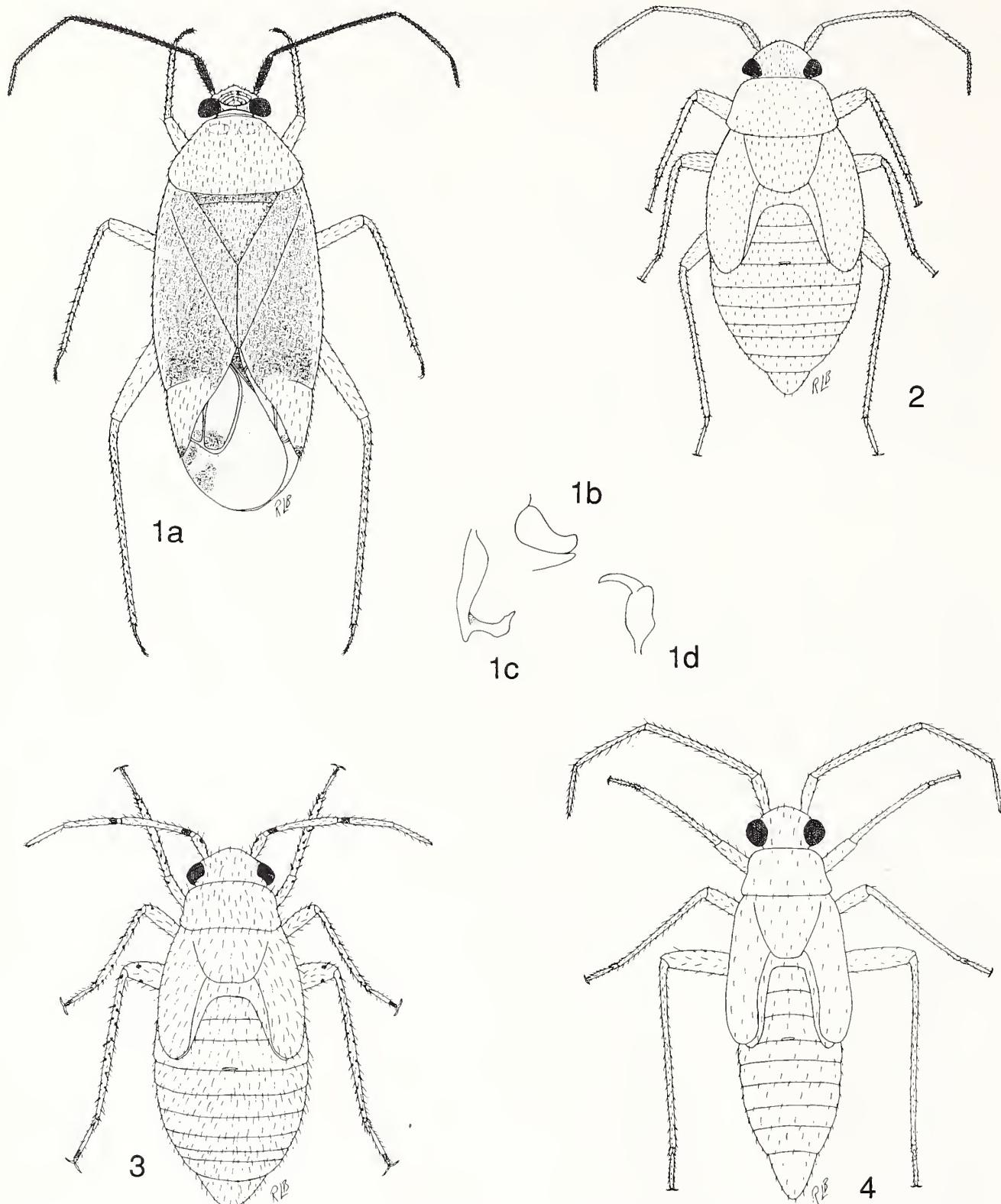
*Adult male* (Fig. 1a). Length 4.83–5.25 (N = 5), width 2.04–2.30. Head: width 0.98–1.03, vertex 0.35–0.38, yellowish, frons with transverse red lines, juga and lora chiefly red, clypeus with basal half yellowish with red streaks, distal half fuscous. Rostrum, length 1.60–1.64, reaching to middle of metacoxae, pale, apex fuscous. Antennae: segment I, length 0.53–0.58, fuscous, dorsal aspect (especially distally) yellowish brown in some specimens; II, 1.65–1.83, fuscous; III, 0.93–1.05, fuscous; IV, 0.50–0.65, fuscous. Pronotum: length 0.95–1.05, width at base 1.73–1.88; uniformly yellowish brown. Scutellum pale yellowish to yellowish brown, transversely striate, mesoscutum reddish. Hemelytra yellowish brown to brown. Embolium and cuneus translucent. Membrane and veins clear to slightly dusky, variously marked with brownish blotches near anal vein, within areoles near their apices and near areoles. Ventral surface pale to yellowish. Fuscous stripe extending from venter of propleura to and including genital segment. Legs pale, apical half of hind femora reddish to fuscous; tibial spines yellowish; third tarsal segment fuscous. Genitalia: Figure 1b–d.

*Remarks.* Males of *L. aesculi* run to *viburni* (Knight) in Knight's (1941) key, but may be distinguished by the black antennal segment II and male genitalia. The left clasper in lateral view is evenly rounded at the angle between the sensory lobe and shaft (*sensu* Schwartz, 1984), whereas in *viburni* the angle is sinuate. In Kelton's (1971) key, *L. aesculi* (Knight) runs to *knighti* Kelton, but may be distinguished by the more uniform yellowish brown color, lack of dark rays behind the calli (present in *knighti*), and by the structure of the male genitalia. The left clasper of *aesculi* lacks the dorsal prongs present in *knighti*.

*Fifth instar* (Fig. 2). Length 3.40–3.96 (N = 5), width 1.60–1.82. Elongate oval, uniformly green, legs and antennae green to yellowish green, tarsal segment II fuscous apically, apex of labial segment IV fuscous. Rather densely clothed with pale, recumbent setae. Head: width 0.85–0.93, vertex 0.45–0.49. Rostrum, length 1.25–1.33, reaching base of mesocoxae. Antennae: segment I, length 0.33–0.36; II, 1.07–1.11; III, 0.82–0.87; IV, 0.45–0.56. Pronotum: length 0.45–0.49, width at base 1.18–1.29. Wing pads reaching abdominal segment IV; dorsal scent gland opening pale, indistinct. Parempodia fleshy, divergent apically.

##### *Microphylellus modestus* Reuter

This mirid is widely distributed in eastern North America, extending from Quebec south to North Carolina and west to Saskatchewan and Texas (Henry and Wheeler, 1988). In addition to Ohio buckeye, *M. modestus* has been recorded from *Acer* sp.,



Figs. 1–4. Fig. 1a–d. *Lygocoris aesculi* adult. 1a. Adult male habitus. 1b. Left paramere, lateral view. 1c. Left paramere, dorsal view. 1d. Right paramere, ventral view. Fig. 2. *Lygocoris aesculi*, fifth-instar nymph. Fig. 3. *Microphylellus modestus*, fifth-instar nymph. Fig. 4. *Orthotylus aesculicola*, fifth-instar nymph.

*Catalpa* sp., *Fraxinus pennsylvanica* Marsh., *Quercus velutina* Lam. (Blinn and Yonke, 1985), *Q. macrocarpa* Michx. (Kelton, 1980), *Carya* sp., *Corylus americana* Walt., *Crataegus mollis* (T. & G.) Scheele, *Q. alba* L., *Ulmus* sp. (Knight, 1941), and *Q. stellata* Wangenh. (Wheeler et al., 1983).

Although adults have been collected from a large number of plants and are believed to breed on *Ulmus* sp., there is no published evidence that any of these plants, other than Ohio buckeye, serve as true breeding hosts. Knight (1941) observed this species on elm leaves curled by aphids, where it fed to some extent on honeydew; less often, he observed it feeding on the eggs of the elm leaf beetle, *Pyrrhalta luteola* (Muller).

*Fifth instar* (Fig. 3). Length 2.15–2.64 (N = 10), width 0.87–1.18. Elongate oval, uniformly green, setigerous spot near apex of antennal segment I, basal annulus on antennal segments II and III, setigerous spot located anteriorly near apex of pro- and mesofemora, metafemora with 2 setigerous spots near apex, 1 anteriorly and a smaller 1 posteriorly, and spots at base of spines on tibiae fuscous. Densely clothed with pale recumbent setae. Head: width 0.55–0.62; vertex 0.31–0.37. Rostrum, length 0.80–0.96, extending to between metacoxae. Antennae: segment I, length 0.16–0.19; II, 0.49–0.55; III, 0.40–0.45; IV, 0.32–0.36. Pronotum: length 0.35–0.39, width at base 0.64–0.75. Wing pads reaching to or slightly beyond abdominal segment IV, dorsal scent gland opening slitlike. Parempodia to setiform, parallel.

#### *Orthotylus aesculicola* Blinn

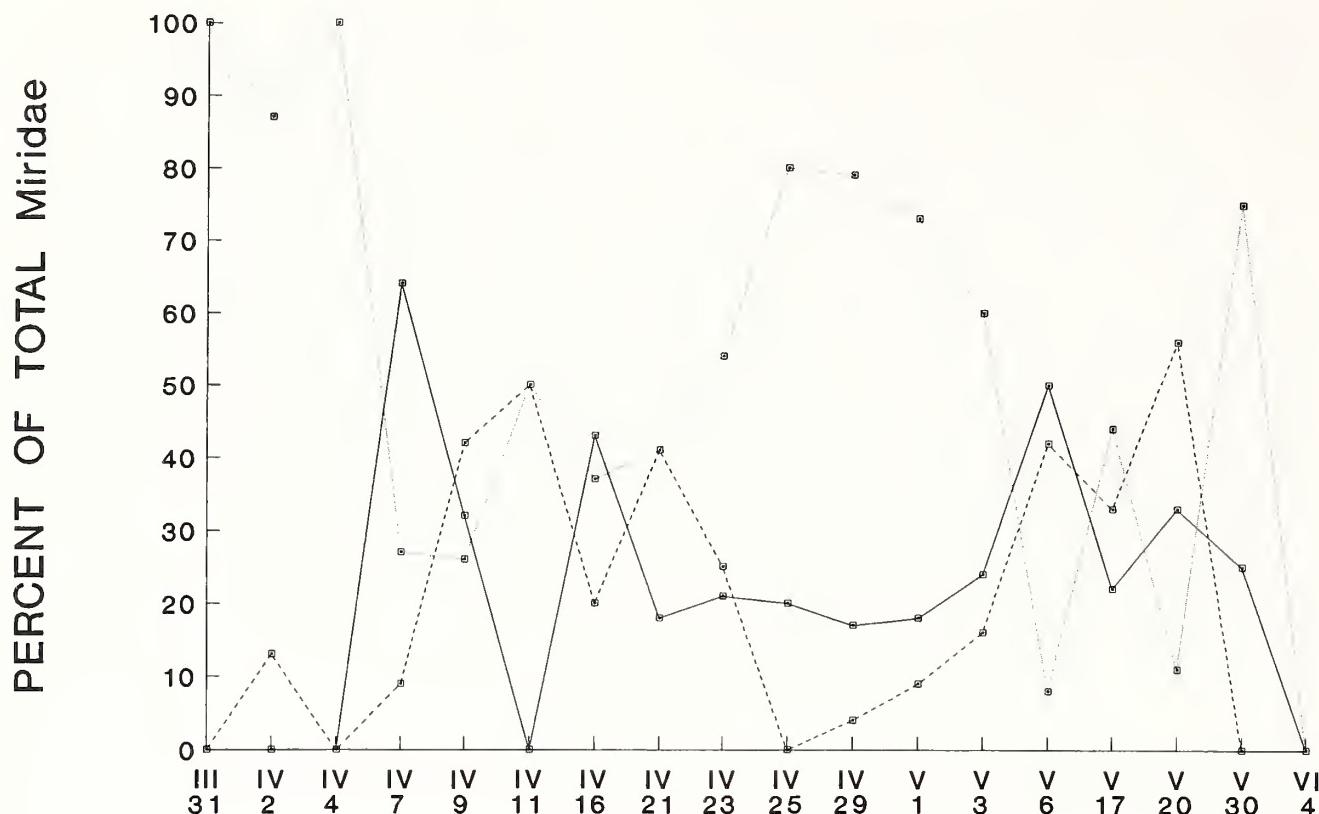
This orthotyline was originally described from material collected in Columbia (Boone Co.), Missouri, on Ohio buckeye by Blinn (1987), who illustrated the adult and male genitalia.

*Fifth instar* (Fig. 4). Length 3.09–3.81 (N = 8), width 0.96–1.16. Elongate slender, uniformly green to yellowish green, head tinged with orange near eyes. Sparsely clothed with pale, recumbent setae. Head: width 0.73–0.76; vertex 0.35–0.44. Rostrum, length 0.98–1.11, extending to apex of mesocoxae. Antennae: segment I, length 0.33–0.38; II, 1.02–1.09; III, 0.69–0.75; IV, 0.49–0.56. Pronotum: length 0.38–0.45, width at base 0.75–0.85. Wing pads reaching abdominal segment IV, dorsal scent gland opening slitlike, anterior area tinged with orange (faded in preserved specimens). Parempodia fleshy, convergent apically.

#### Seasonal History

Sampling results are given in Figures 5 and 6. Figure 5 gives the percentage of all stages of each species relative to the total number of Miridae collected per sampling date. Figure 6 shows the immatures and adults of each species separately as a percentage of the total immature, and adult catch, respectively, per sampling date.

The life cycles of these 3 species are similar and can be summarized as follows. All three species were present from late March or early April to the end of May, with almost complete overlap among the species (Fig. 5). Overwintering eggs begin to hatch from late March to early April, coinciding with leaf flush and the onset of flowering. All instars of these species are active feeding stages, and development takes place during a time when the host plant is producing new growth and flowers. Early instars (I–III) of both *L. aesculi* and *O. aesculicola* were observed feeding on the expanding leaflets and flowers where, with their uniform green color, they resembled the color of the young foliage and flowers. Later instars (IV–V) and adults of *L. aesculi* and *O. aesculicola* were observed feeding on both the flowers and leaves at about equal frequencies, with the former species preferring the flowers and the latter species the underside of leaves. Feeding by *M. modestus* was not observed.



### SAMPLING DATES (1985 & 1986)

Fig. 5. Seasonal occurrence of the three species of Miridae on *Aesculus glabra* during 1985 and 1986. Adults and immatures combined for each plant bug species. Solid line = *Lygocoris aesculi*; dotted line = *Microphylellus modestus*; dashed line = *Orthotylus aesculicola*.

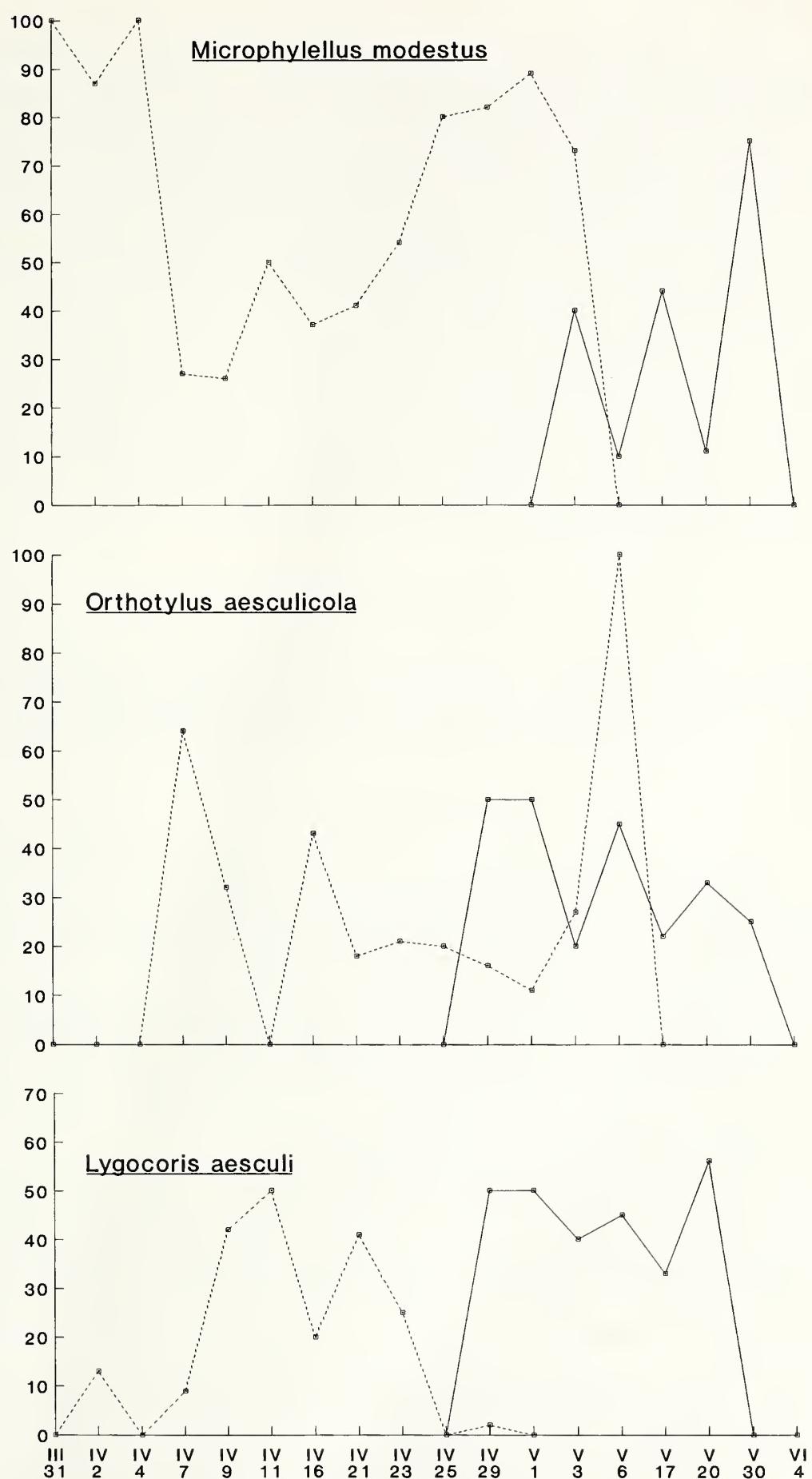
Developmental time from first instar to the adult molt takes ca. 3.5 to 4.5 weeks, with each of the 5 nymphal instars taking from 4 to 7 days. Adults can be found in the field for 3 to 4 weeks following eclosion from late April through May where they mate and the females deposit the overwintering eggs. By late May or early June the active portion of the life cycle of these mirids has ended, with the eggs overwintering to complete the life cycle. There was no evidence of more than a single generation per year for each species, which is consistent with what has been reported for congeners (Knight, 1917; Pinto, 1982; Southwood and Leston, 1959; Wheeler, 1982).

*M. modestus* was the first species to appear in the sampling. First instars were present from 31 March to 4 April. Instars II and III were first collected on 7 April, and 9 April, respectively and were present until 21 April and 25 April, respectively. Fourth instars were collected only from 21 April to 23 April. Fifth instars were present from 23 April to 3 May. Adults first appeared in the samples on 3 May and were present until 30 May.

For *L. aesculi* the earliest specimen observed was a first instar collected on 2 April

Fig. 6. Seasonal occurrence of the three species of Miridae on *Aesculus glabra* during 1985 and 1986. Dotted lines indicate immatures, solid lines adults.

PERCENT OF TOTAL IMMATURE/ADULT Miridae



SAMPLING DATES (1985 &amp; 1986)

1986. First instars were present from 2 April through 9 April. Instars II to IV were present from 9 April through 16 April, 11 April, and 30 April, respectively. Fifth instars were present from 11 April through 23 April. Adults began to appear during the last week of April and were present only for 3–4 weeks; the last male was collected on 17 May, the last female on 21 May. In the sampling, adults of this univoltine mirid were no longer present after 21 May in 1985 and 20 May in 1986.

For *O. aesculicola* instars I to III were first collected on 7 April and were present through 16 April for the first instar and 21 April for both instars II and III. Fourth instars were present in the samples from 16 April through 30 April. Fifth instars were present from 23 April through 6 May. Adults first appeared during the last week of April and were present for ca. 4 weeks. In the sampling, adults of this univoltine mirid were no longer present after 30 May in 1985 and 20 May in 1986.

No sign of damage was observed in the field as a result of feeding by these 3 plant bug species, perhaps due to their low population densities. In the laboratory, both nymphs and adults failed to produce any visible damage when confined to unblemished leaves of Ohio buckeye.

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**PRIAPISMUS PINI, A NEW SPECIES OF  
DISCOCEPHALINI FROM HONDURAS ON PINE  
(HEMIPTERA: PENTATOMIDAE: DISCOCEPHALINAE)**

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*Abstract.*—A new species of pentatomid, *Priapismus pini*, is described from Honduras. Both nymphs and adults were collected on *Pinus maximinoi* H. E. Moore.

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The genus *Priapismus* Distant, 1889, ranges from Ecuador to Honduras and currently contains five species (Rolston, 1984). None of the species is commonly collected, and there has been no host record for any of them until now. Several nymphal instars as well as adults of the species described here were collected under the bark of *Pinus maximinoi* H. E. Moore in Honduras. Although the trees were stressed and covered with sooty mold, the bug's role in this situation is unclear.

***Priapismus pini*, new species**

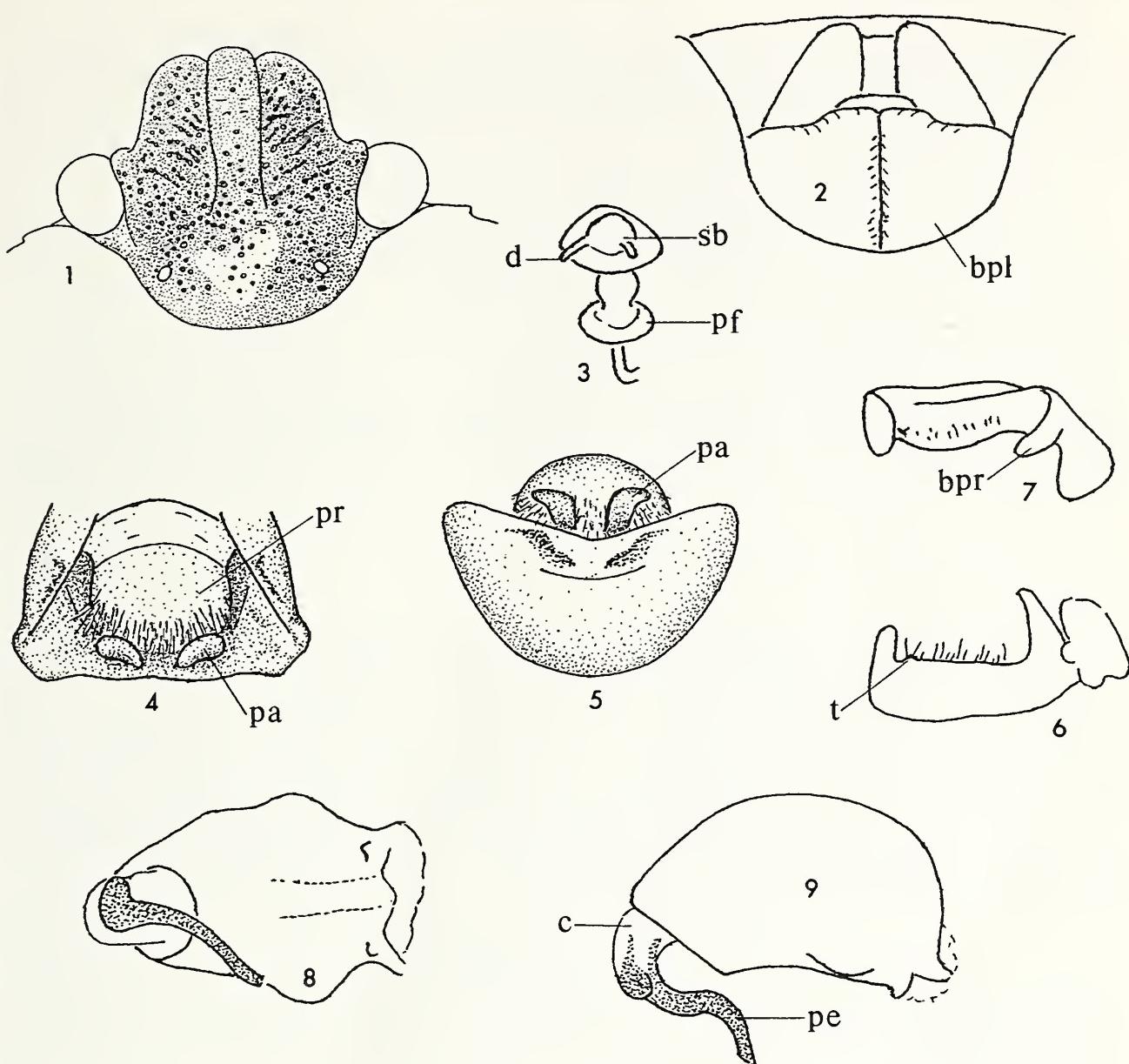
Flavescence ground color of dorsum largely obscured on head, pronotum and scutellum by black punctuation and suffusion from punctures; ground color predominant on coria. Rufous flecks often present in some pale areas of dorsum, especially along R+M vein of each corium and on midline of pronotum. Venter predominantly black with small, pale markings, especially on lateral borders of abdomen.

Head densely punctate including tylus or at least postclypeal part (Fig. 1). Vertex sometimes bearing small, flavescence, irregularly shaped macule partially surrounding cluster of black punctures. Each antenna black excepting superior surface of basal segment, joints between segments, and basal or subbasal band of fifth segment pale. First two segments of rostrum flavescence, third somewhat infuscated basally, fourth darkening gradually to black apically; apex reaching to or onto fourth visible abdominal sternite.

Pronotum consistently marked with pale, mesial vitta of very irregular outline; other pale markings on pronotal disk consisting of scattered, usually small macules.

Scutellum consistently marked with pale callus adjacent to fovea in each basal angle; fovea black, punctate. Scutellar apex with three inconspicuous, pale macules, one mesial and one on each side just cephalad of mesial macule; these lateral macules may meet, forming transverse bar, or all three macules become confluent, forming Y. Additional small, pale macules usually present on scutellar disk, particularly on midline.

Each corium bearing large, black macule at distal end of R+M vein; punctuation moderately strong, irregular, black, tending to form blotches on endocorium; membrane lightly fumose, its four vestigial veins darker. Connexiva moderately exposed, alternated flavescence and black with black bordering both sides of transverse sutures.



Figs. 1–9. *Priapismus pini*. 1. Head. 2. Genital plates. 3. Spermathecal bulb and pump. 4. Genital cup. 5. Pygophore, caudal view. 6. Paramere, lateral view. 7. Same, rotated ca. 90° toward viewer. 8. Phallotheca, ventral view. 9. Same, right lateral view. Symbols: bpl, basal plate; brp, basal projection; c, conjunctiva; d, diverticulum; pa, paramere; pe, penisfilum; pf, proximal flange; pr, proctiger; sb, spermathecal bulb; t, tubercle.

Venter predominately fuscous; head except bucculae sometimes extensively flavescent; posterolateral border of each metapleuron and middle of lateral margins of each abdominal sternite flavescent; a few small macules usually scattered elsewhere on venter. Legs flavescent, heavily marked with fuscous spots and macules. Abdominal venter impunctate mesially; lateral punctuation becoming denser and stronger as far as spiracles, then weaker. Spiracles and surrounding area fuscous.

**Measurements** (mm, both sexes). Total length 6.8–7.5. Width of head 1.75–1.90, length 1.20–1.35, length to ocelli 0.95–1.05; interocular width 1.00–1.15; width across ocelli 0.80–0.90. Segments 1–5 of antennae: 0.30–0.35; 0.30–0.40; 0.55–0.70; 0.65–0.75; 1.00–1.10. Segments 1–4 of rostrum: 0.75–0.95; 1.00–1.15; 0.90–1.00; 1.10–1.15. Pronotal width 3.5–3.9, mesial length 1.6–1.8. Scutellar width at base 2.4–2.6, width at distal end of frena 1.6–1.8, length 3.1–3.5.

*Genitalia.* ♀. Posterior margin of basal plates sigmoid from caudoventral view, border curving abruptly dorsad from disk; mesial margin of each plate raised in narrow ridge, adjacent half of disk slightly impressed (Fig. 2). Spermathecal duct simple; sclerotized duct of spermathecal pump constricted distad of proximal flange (Fig. 3); spermathecal bulb globose, bearing three short diverticula.

♂. Proctiger largely covering genital cup, rather thickly clothed distally with moderately long hairs, widely separated by membrane from anterior margin of genital cup (Fig. 4). Only flattened, distal ends of parameres visible in cup. Pygophore noticeably impressed adjacent to anterolateral rim of genital cup; posterior pygophoral margin sinuously transverse from dorsal view, widely and shallowly emarginate from caudal view (Fig. 5). Each paramere with large, compressed, basal projection; apex flattened and bent dorsolaterad; small, setose tubercle located on shaft near apical bend (Fig. 6); shaft essentially triangular with many small hairs on dorsal surface (Fig. 7). Phallotheca without appendages; penisfilum sigmoid, asymmetrically flanged where conjunctiva joins (Figs. 8, 9); conjunctiva lacking diverticula.

*Types.* Holotype, male labeled "Honduras: Cortes St. Cusuco Nat. Park[.] 26 I 1991[.] On Pinus maximinoi[.] Coll: R.S. Cameron." Deposited in National Museum of Natural History, Washington, D.C. Paratypes: 4 males, 5 females with same labeling as holotype. Punctuation in brackets is not on labels.

*Comments.* This species is most like *P. costaricensis* Rolston, 1984, a species described from females. Measurements of these two species are quite similar, but their color and punctuation are dissimilar. *P. pini* is the only known species of the genus that is predominantly dark in color, and the denser punctuation, particularly on the head, separates it from *P. costaricensis*.

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## LIFE HISTORY AND DESCRIPTIONS OF THE IMMATURE STAGES OF THE PLANTHOPPER *PROKELISIA CROCEA* (VAN DUZEE) (HOMOPTERA: DELPHACIDAE)

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*Abstract.*—The life history of *Prokelisia crocea* (Van Duzee) was studied in Missouri from May to October 1988 and the immature stages described. *P. crocea* feeds and reproduces on prairie cordgrass, *Spartina pectinata* Link, is trivoltine and overwinters as nymphs. Nymphal instars differed in body size, development of wingpads, number of metatibial spines, and shape and dentition of metatibial spurs.

Extensive ecological studies of two of the five species of *Prokelisia*, *P. marginata* (Van Duzee) and *P. dolus* (Wilson), have focused on laboratory rearing, nutrition, parasites, predators, and wing morphology (literature summarized in Denno et al., 1985, 1986). The host plants of these salt marsh species are *Spartina alterniflora* Loisel and *S. foliosa* Trin. No information is available on the biology of planthoppers occurring on the inland species of *Spartina*, *S. pectinata* Link.

*Prokelisia crocea* (Van Duzee) is monophagous on prairie cordgrass (*S. pectinata*) and has been recorded from Maine south to Connecticut, and west to North Dakota and New Mexico (Metcalf, 1943; Wilson, 1982). Wilson (1982) and Heady and Wilson (1990) provided detailed descriptions of male and female adults of *P. crocea*.

The present study summarizes the life history of *P. crocea* on prairie cordgrass in Missouri, and provides information on laboratory rearing and descriptions and illustrations of immature stages with a key to nymphal instars.

### MATERIALS AND METHODS

*Field study.* The field study was conducted on plots of *Spartina pectinata* along roadsides and native tallgrass prairies in Saline, Pettis, and Johnson Counties, Missouri. Weekly sweep and D-vac suction samples (Holder and Wilson, in prep.) were taken from 24 May to 10 October 1988 and 26 April to 11 May 1989. Some specimens were placed in vials and returned to the laboratory for rearing. Most were preserved in 70% isopropyl alcohol for phenological analysis, measurements and descriptions. Information recorded from these samples included number of individuals captured and number of each nymphal instar. Feeding and oviposition sites were determined, in both field and laboratory studies, by observing individuals on the host plants. Attempts were made to collect overwintering nymphs by gathering thatch from host plant sites in five 20-gallon plastic garbage bags in February, March, November and December, 1989, and placing it in a large modified Berlese funnel; these samples produced no planthoppers. A further attempt at collecting specimens with a modified leaf vacuum (Wilson et al., in prep.) was made on 24 November 1990.

*Laboratory study.* Plants were collected from roadside areas and potted in 12 cm

diam pots. An environmental chamber was unavailable thus plants were maintained in a laboratory under fluorescent lights on a 12-hr light-dark cycle; temperature ranged from 18 to 32°C. Adults were collected and placed on potted plants (Calvert and Wilson, 1986), nymphs were collected and placed on individual plants but survival was poor. Immatures were also placed in 2.5 cm diam culture tubes containing a fresh *S. pectinata* leaf and plugged with cotton (Calvert et al., 1987). Insufficient data were collected to determine stadia of nymphal instars due to low survival of nymphs.

The 5th instar is described in detail but only major differences are described for 4th through 1st instars. Measurements are given in mm as mean  $\pm$  SD. Length was measured from apex of vertex to apex of abdomen, width across the widest part of the body, and thoracic length along the midline from the anterior margin of the pronotum to the posterior margin of the metanotum. Eggs were obtained by excising them with a fine needle from the potted host plants.

#### RESULTS AND DISCUSSION

*Field study.* *P. crocea* is trivoltine in Missouri and overwinters as fifth instar nymphs which were collected on 24 November and 26 April (Figs. 1, 2). Adults were found from 26 April to 9 June and 23 June to 20 September. First instar nymphs were first collected on 9 June and found sporadically until 2 October. Second through fifth instar nymphs showed similar seasonal distributions.

Nymphs and adults were observed feeding along the midrib on the axial surface of leaves near the base of the leaf and on the stem. Two percent of adult *P. crocea* ( $N = 100$ ) were found to be brachypterous.

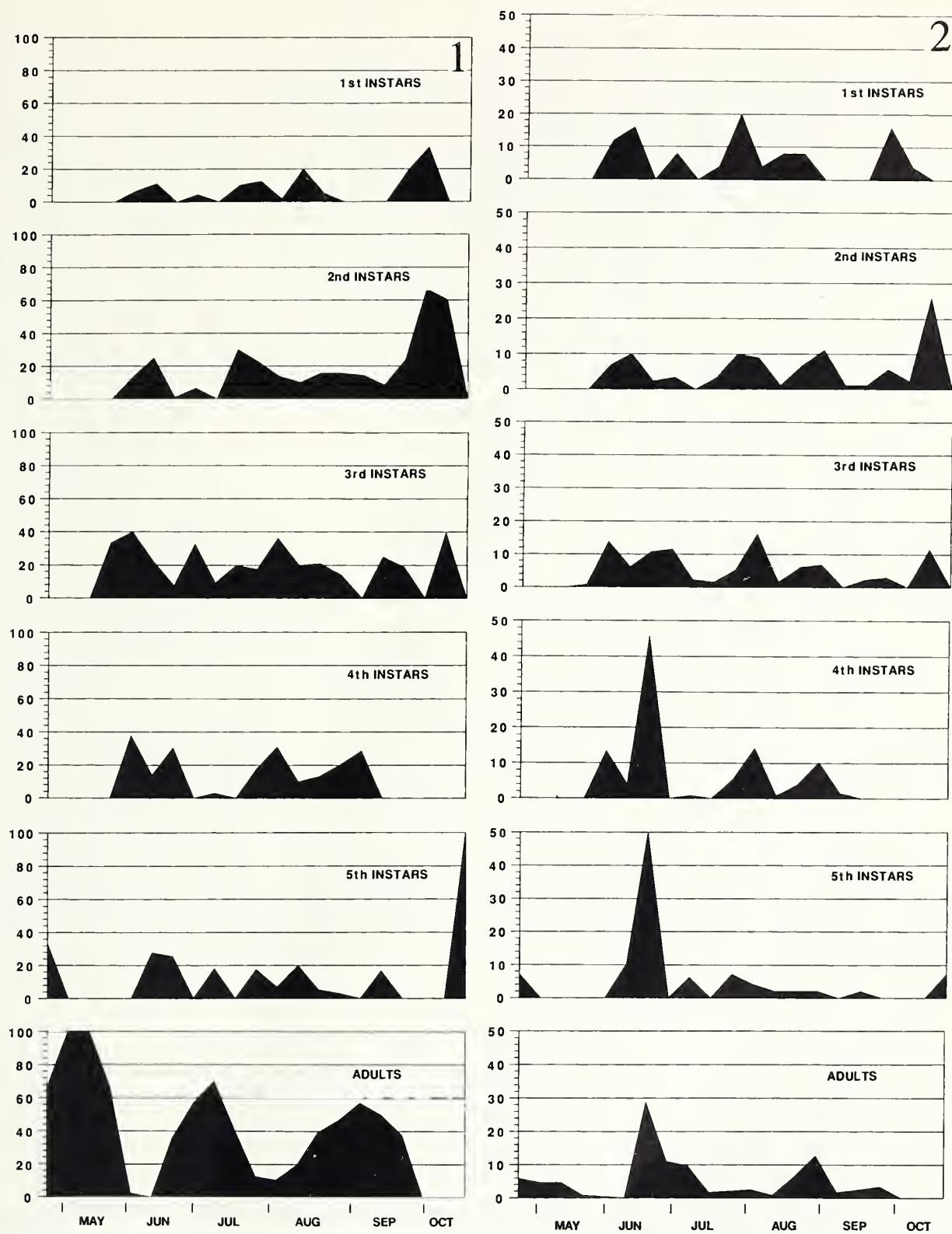
*Laboratory study.* Numerous attempts to rear field collected specimens on potted *S. pectinata* in the laboratory were only partially successful. Because an incubator was unavailable, plants were kept in a laboratory where low humidity apparently reduced survival of nymphs during hatching and ecdysis.

Females deposit eggs singly in slits made with the ovipositor along the midrib of either the axial or adaxial surface of a leaf. After eggs have been inserted into the plant tissue they are covered with wax from the 9th abdominal tergite.

*Descriptions.* *Fifth instar* (Figs. 3–6, 16). Length  $2.7 \pm 0.21$ ; thoracic length  $0.9 \pm 0.09$ ; width  $0.9 \pm 0.13$ .  $N = 13$ .

Body straw color with white middorsal line extending from vertex almost to end of the abdomen. Form elongate, subcylindrical, slightly flattened dorsoventrally, widest across mesothoracic wingpads.

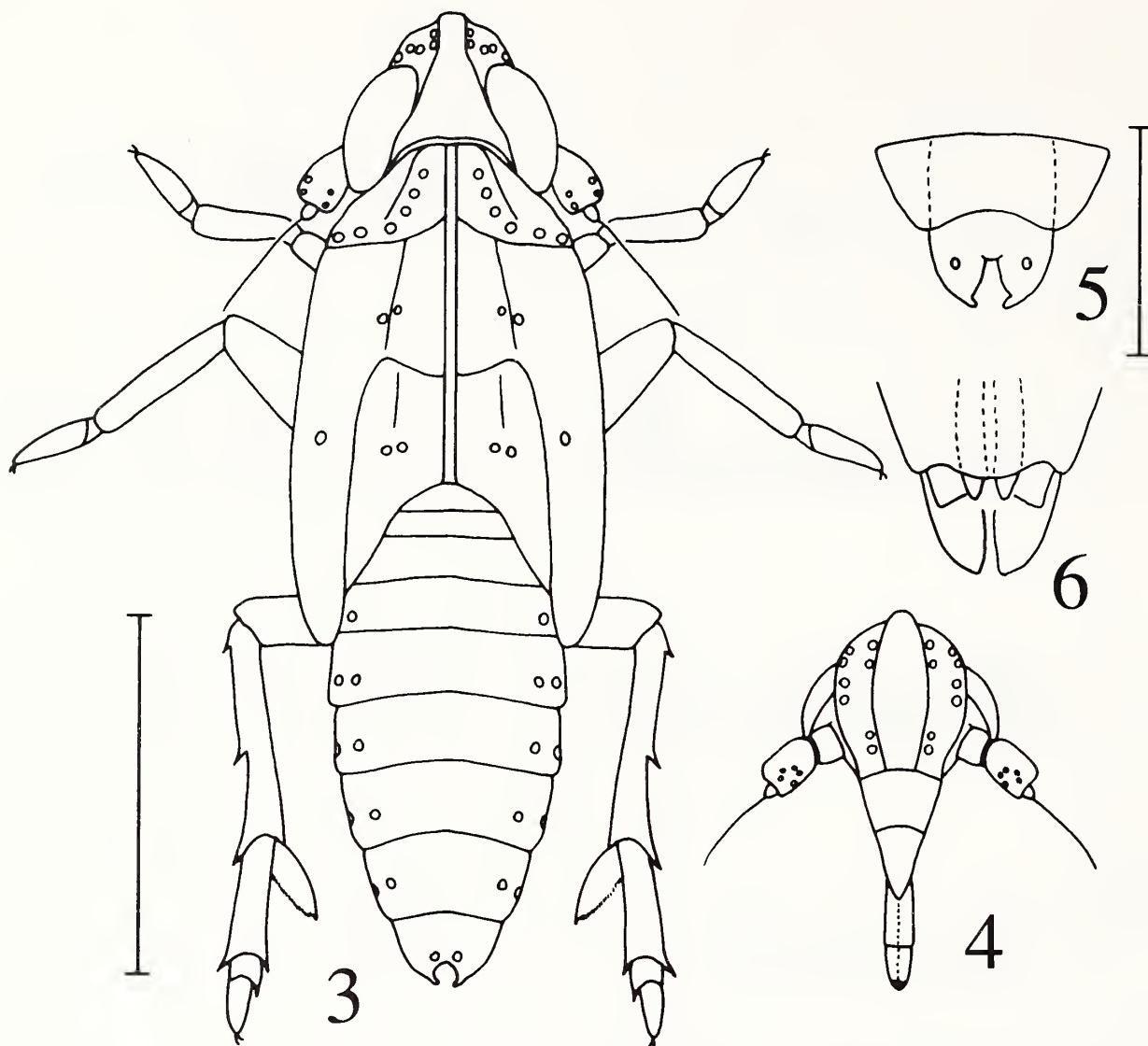
Vertex subtriangular, narrowing anteriorly; posterior margin concave, lateral margins concave in anterior  $\frac{1}{2}$ . Frons yellowish with white longitudinal median line; border with clypeus slightly convex; lateral margins convex and carinate (outer carinae) and paralleled by second pair of carinae (inner carinae) continuous with lateral margins of vertex; area between inner carinae forming trough; area between inner and outer carinae with 9 pits on each side (8 visible in frontal view); 4 pits between each outer carina and eye. Clypeus yellow, narrowing distally, consisting of subconical basal postclypeus and cylindrical distal anteclypeus. Beak 3-segmented, cylindrical, segment 1 hidden by anteclypeus, segment 2 ca.  $1.3 \times$  length of segment 3, segment 3 with black apex. Antennae 3-segmented; scape short, cylindrical; pedicel subcylindrical,  $2 \times$  length of scape, with ca. 8–10 pit-like sensoria; flagellum bulbous basally,



Figs. 1-2. Seasonal occurrence of *P. crocea* in Missouri. 1. Number of individuals of each stage is expressed as percentage of total individuals of all stages collected per collection date. 2. Number of individuals of each stage is expressed as percentage of all individuals of that stage collected throughout the study ( $N_A = 236$ ,  $N_5 = 98$ ,  $N_4 = 127$ ,  $N_3 = 130$ ,  $N_2 = 89$ ,  $N_1 = 25$ ).

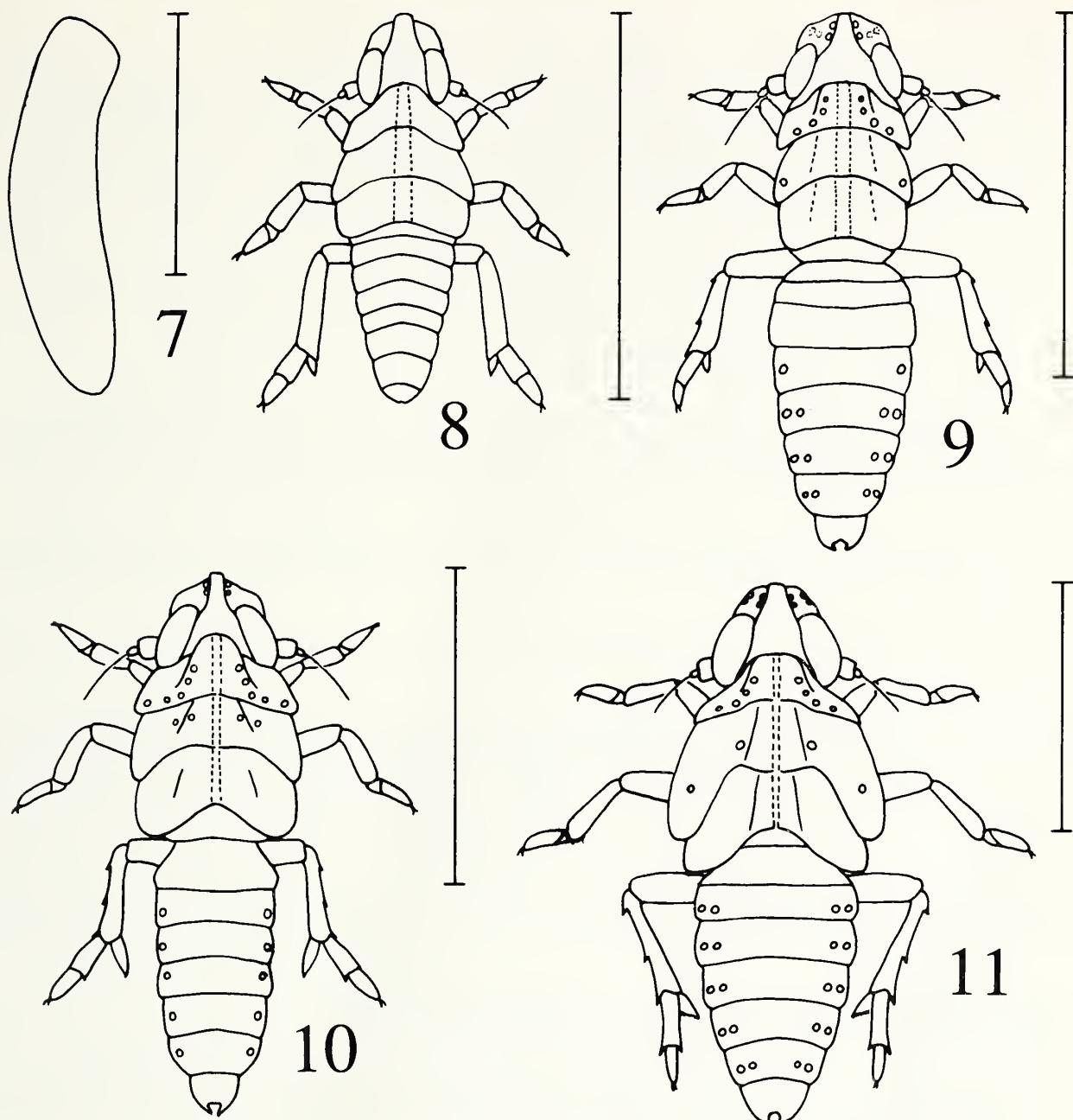
with elongate bristle-like extension distally, bulbous base ca.  $0.2 \times$  length of pedicel. Eyes red.

Thoracic nota divided by middorsal line into three pairs of plates. Pronotal plates subtriangular; anterior margin convex following posterior border of eye; posterior



Figs. 3–6. *P. crocea* fifth instar. 3. Habitus. 4. Frontal view of head. 5. Apical part of venter of male abdomen. 6. Apical part of venter of female abdomen. Vertical bar = 1.0 mm (3, 4); = 0.5 mm (5, 6).

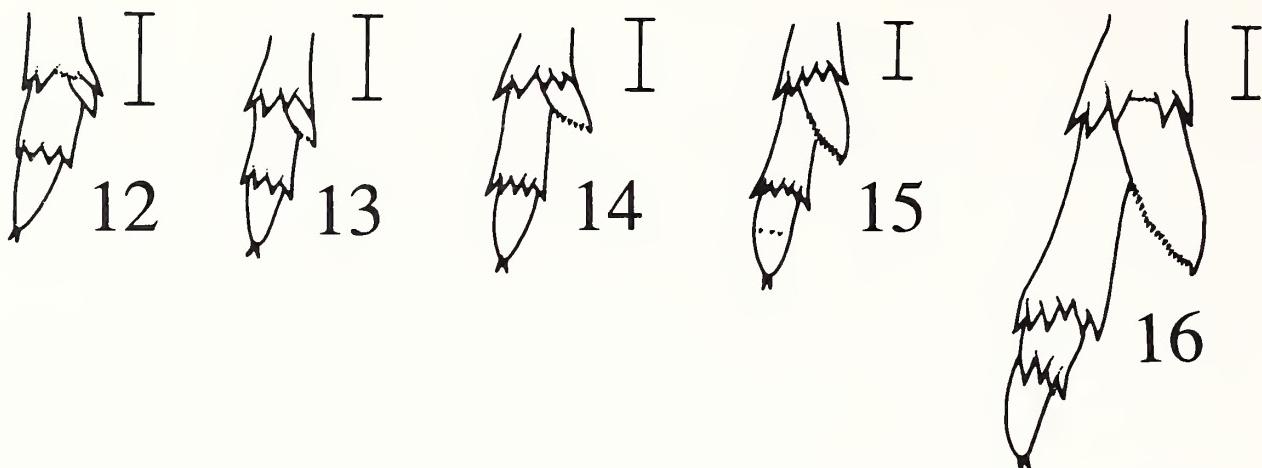
border sinuate; each plate with row of 7 pits originating at anterior margin curving distally from middorsal line to lateral margin (lateralmost pits often not visible in dorsal view). Mesonotum with median length  $1.5 \times$  that of pronotum; subrectangular; elongate lobate wingpads extending to tips of metanotal wingpads; each plate with posterolaterally directed carina originating on anterior margin in median  $\frac{1}{4}$  and terminating on posterior margin in lateral  $\frac{1}{2}$ ; area between carinae elevated and triangular; 2 pits near carina and 1 pit on lateral  $\frac{1}{3}$ . Metanotum with median length ca.  $1.25 \times$  that of mesonotum; subrectangular, lobate wingpads extending to middle of 4th tergite; each plate with weak longitudinal carina and 2 pits near middle of plate. Pro- and mesocoxae elongated and directed posteromedially; metacoxae fused to sternum. Metatrochanter short and subcylindrical. Pro- and mesofemora and tibiae with 2 ventral and 1 dorsal longitudinal rows of setae. Metatibia with 2 spines on lateral aspect of shaft, an apical transverse row of 5 black-tipped spines on plantar surface and a subtriangular flattened movable spur with 13–14 teeth on posterior margin. Pro- and mesotarsi with 2 tarsomeres, tarsomere 1 wedge-shaped; tarsomere



Figs. 7-11. *P. crocea* immature stages. 7. Egg. 8. First instar. 9. Second instar. 10. Third instar. 11. Fourth instar. Vertical bar = 0.5 mm (7); = 1.0 mm (8-11).

2 subconical, ca. 4× length of tarsomere 1, with pair of apical claws and median membranous pulvillus. Metatarsi with 3 tarsomeres; tarsomere 1 with apical transverse row of 6 black tipped spines on plantar surface; tarsomere 2 cylindrical, ca. 4× length of tarsomere 1, with apical transverse row of 4 black tipped spines on plantar surface; tarsomere 3 subconical, ca. 2× length of tarsomere 2 with pair of apical claws and median pulvillus.

Abdomen 9-segmented; slightly flattened dorsoventrally; widest across 5th abdominal segment. Tergite 1 small, subtriangular; 2 subrectangular, ca. 0.5× width of 3; tergites 4-8 each with 2 lateral pits on either side (lateralmost pits not always visible in dorsal view). Segment 9 surrounding anus, with 3 pits; female with 1 pair of acute processes extending from juncture of sternites 8 and 9; males lacking processes.



Figs. 12–16. *P. crocea* apices of metathoracic legs. 12. First instar. 13. Second instar. 14. Third instar. 15. Fourth instar. 16. Fifth instar. Vertical bars = 0.1 mm.

*Fourth instar* (Figs. 11, 15). Length  $2.1 \pm 0.26$ ; thoracic length  $0.7 \pm 0.06$ ; width  $0.7 \pm 0.09$ . N = 11.

Antennal pedicel with 4–6 sensoria; basal portion of antennal flagellum  $0.3 \times$  length of pedicel.

Mesonotal wingpads shorter, each covering ca.  $\frac{2}{3}$  of metanotal wingpad laterally. Metanotal median length  $1.125 \times$  that of mesonotum; carinae weaker; wingpad extending to tergite 2. Metatibial spur slightly smaller, with 8–10 teeth on margin. Metatarsi with 2 tarsomeres; tarsomere 1 with apical transverse row of 6 black-tipped spines on plantar surface; tarsomere 2 subconical with 3 black-tipped spines in middle of tarsomere on plantar surface.

*Third instar* (Figs. 10, 14). Length  $1.8 \pm 0.14$ ; thoracic length  $0.6 \pm 0.09$ ; width  $0.6 \pm 0.06$ . N = 11.

Basal flagellum of antenna ca.  $0.5 \times$  length of pedicel.

Mesonotal wingpads shorter, each covering  $\frac{1}{3}$  of metanotal wingpad laterally. Metanotal wingpad extending to juncture of tergites 1 and 2. Metatibial spur smaller; with 5 marginal teeth. Metatarsomere 1 with apical transverse row of 5 black-tipped spines on plantar surface.

*Second instar* (Figs. 9, 13). Length  $1.4 \pm 0.15$ ; thoracic length  $0.4 \pm 0.08$ ; width  $0.4 \pm 0.07$ . N = 13.

Mesonotal plates each with 1 pit; wing pads undeveloped. Metanotal wingpads undeveloped. Metatibia with apical row of 4 black-tipped spines on plantar surface; spur small with 3 marginal teeth, ca.  $3 \times$  length of longest metatibial spine; metatarsomere 1 with 4 apical black-tipped spines.

*First instar* (Figs. 8, 12). Length  $1.1 \pm 0.15$ ; thoracic length  $0.3 \pm 0.04$ ; width  $0.2 \pm 0.05$ . N = 15.

Bulbous base of antennal flagellum subequal in length to that of pedicel.

Metatibia lacking spines on shaft, with apical row of 3 black-tipped spines on plantar surface; metatibial spur smaller, ca.  $1.5 \times$  length of longest metatibial spine, lacking marginal teeth.

*Egg* (Fig. 7). Length  $0.7 \pm 0.05$ ; width  $0.2 \pm 0.02$ . N = 8.

Eggs laid singly; white; cylindrical, slightly flattened; curved in anterior  $\frac{1}{4}$ ; chorion translucent, smooth.

KEY TO *P. CROCEA* NYMPHAL INSTARS

1. Metatibial spur with more than 7 marginal teeth; mesonotal wingpads overlapping more than half length of metanotal wingpads (Figs. 3, 11, 15, 16) ..... 2
- Metatibial spur with fewer than 7 marginal teeth; mesonotal wingpads overlap less than half length of metanotal wing pads (Figs. 8–10, 12–14) ..... 3
2. Metatarsi with 3 tarsomeres; metatibial spur with more than 11 marginal teeth (Fig. 16) ..... 5th Instar
- Metatarsi with 2 tarsomeres; metatibial spur with fewer than 11 marginal teeth (Fig. 15) ..... 4th Instar
3. Metatibia with transverse row of 5 apical spines, spur with 5 marginal teeth (Fig. 14) ..... 3rd Instar
- Metatibia with fewer than 5 apical spines, spur with fewer than 5 marginal teeth (Figs. 12, 13) ..... 4.
4. Metatibia with 2 lateral spines on shaft and 4 apical spines, spur with 3 marginal teeth (Fig. 13) ..... 2nd Instar
- Metatibia without lateral spines on shaft and with 3 apical spines, spur without marginal teeth (Fig. 12) ..... 1st Instar

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A UNIQUE *AMYCLE* NYMPH (HOMOPTERA: FULGORIDAE)  
THAT MIMICS JUMPING SPIDERS  
(ARANAEAE: SALTICIDAE)

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*Abstract.*—An undescribed *Amycle* fulgorid planthopper nymph that mimics jumping spiders when viewed from behind is recorded from Guerrero, Mexico. The nymph has 4 smooth, polished dark areas on its metathorax and hind wing pads that resemble the anterior eyes of jumping spiders. The middle and hind legs, which project posteriorly and have flattened femora and tibiae, were moved in an up and down manner similar to those of salticid legs and pedipalpi. It is hypothesized that such mimicry affords protection from predation by salticids only, not predators in general.

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Many spiders mimic insects, especially ants (Reiskind, 1970, 1977; Edmunds, 1978; Foelix, 1982; Jackson, 1982), but the converse has only been observed in the fly family Tephritidae. Monteith (1972) commented on the similarity in appearance and behavior between the apple maggot *Rhagoletis pomonella* (Walsh), the cherry fruit fly *R. cingulata* (Loew) (Tephritidae), and the sympatric jumping spider *Paraphidippus marginatus* (Walck.) (Salticidae). Eisner's (1985) report that the tephritid *Zonosemata vittigera* (Coquillett) mimicked jumping spiders stimulated a flurry of experiments dealing with the protection afforded by spider mimicry (Mather and Roitberg, 1987; Greene et al., 1987; Whitman et al., 1988).

It has been suggested, but never demonstrated, that other insects also may mimic spiders. O'Brien (1967) reported the behavior and appearance of male *Caliscelis bonellii* (Latreille) (Homoptera: Issidae) strongly resembled that of jumping spiders. Santiago-Blay and Maldonado-Capriles (1988) suggested *Emesa tenerrima* (Dohrn) (Hemiptera: Reduviidae) may mimic the spider *Modisimus signatus* (Banks) (Pholcidae) in Puerto Rico.

I report here a nymph of *Amycle* sp. (Homoptera: Fulgoridae) which closely resembles a salticid spider when viewed from behind. The single specimen, a fourth instar nymph, was collected by sweep-netting in a dryland forest 4.5 miles northwest of El Ocotito, Guerrero, Mexico, on July 7, 1987, by R. A. Wharton. Although seven entomologists were collecting in the area, only the single specimen was caught.

The mimic has four smooth, polished dark areas on the metathorax which imitate the anterior eye row of a salticid, even to the point of reflecting highlights (Figs. 1–3). Furthering the illusion are the middle and hind legs with flattened femora and tibiae. These project posteriorly and simulate the anterior legs and pedipalpi of a jumping spider. The specimen, which is 7.2 mm long and 3.9 mm wide, is approximately the same size as the largest salticid collected from the same locality (Fig. 4). This fulgorid nymph was observed moving its middle and hind legs up and down in a manner similar to that of a salticid courtship or aggression display. The fulgorid was killed and preserved in 70 percent ethanol, critical-point dried, and mounted



Fig. 1. Posterior view of *Amycle* sp. spider mimic.

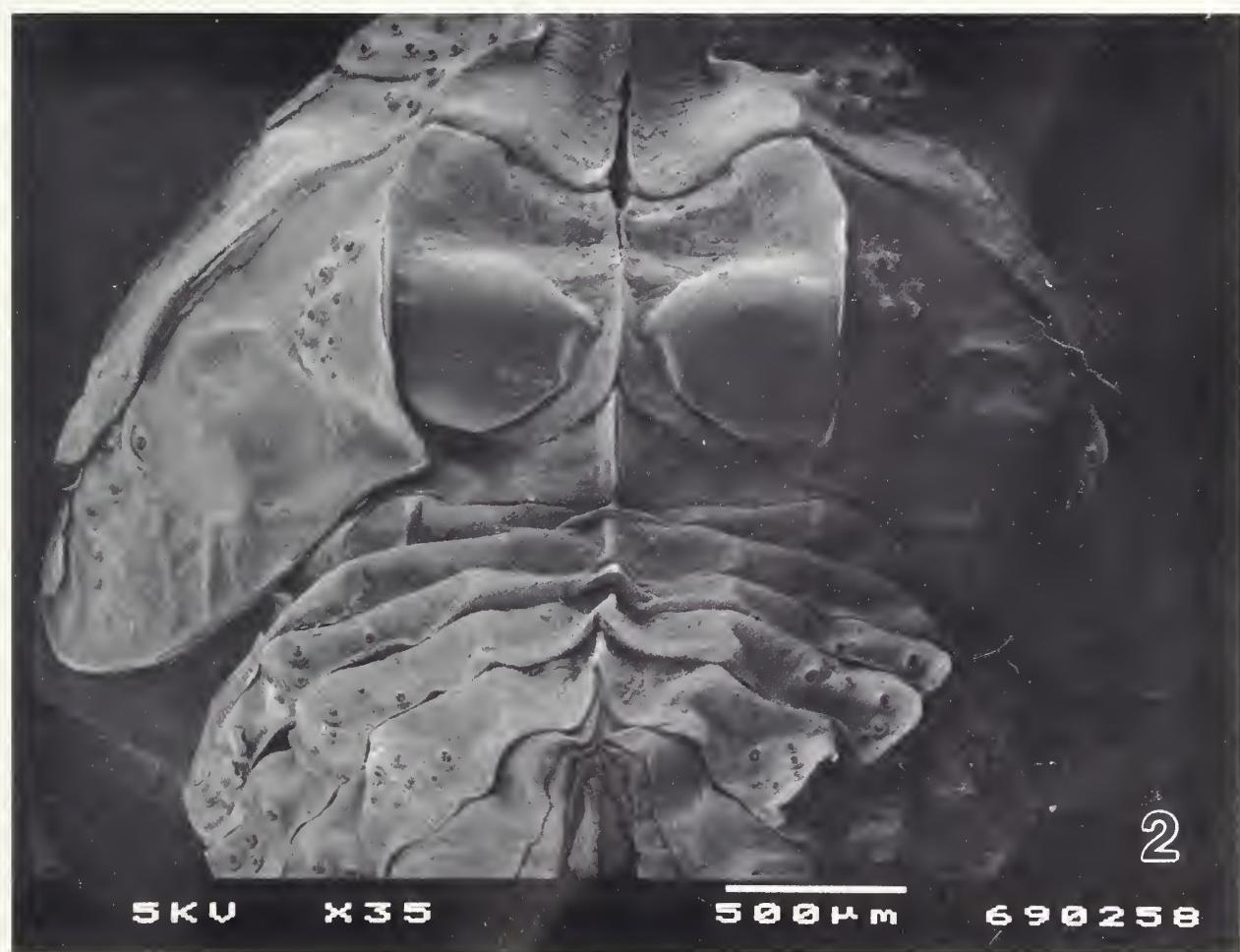


Fig. 2. Posterior view of metathorax and abdomen of *Amycle* sp. showing smooth areas that imitate salticid eyes.



Fig. 3. Posterior dorsal view of *Amycle* sp.

for 35 mm photography. The mimic has been deposited as Voucher Specimen No. 554 in the Texas A&M University Insect Collection. Five earlier instar nymphs of *Amycle* sp. were collected screen-sweeping the area. They lack the flattened femora and tibiae and false eyes of the spider mimic and are not believed to be conspecific with the mimic.

Jumping spiders were the most common cursorial spider collected by screen-sweeping the habitat. All spiders collected were approximately the same size or smaller than the mimic. Salticids present at the collection site were: *Habronattus zebranus* F.O.P.C., *Habronattus* sp., *Metaphidippus* sp., *Nycerella delecta* (Peckhams), *Peckhamia* sp., and *Thiodina* sp. Other cursorial spiders collected from the same habitat were: *Strotarchus* sp. (Clubionidae), *Oxyopes* sp. (Oxyopidae), *Apollophanes* sp. nr. *punctipes* F.O.P.C. (Philodromidae), *Misumenoides* sp., *Misumenops* sp. nr. *dubius* (Keyserling), and *Xysticus facetus* F.O.P.C. (Thomisidae).

As only the single specimen was collected and observed for a short period, it is unknown whether the mimic is modelled after a specific salticid species or jumping



Fig. 4. *Amycle* sp. and the salticid *Nycerella delecta* (Peckhams) collected from the same locality.

spiders in general. Also unknown is whether such mimicry affords protection from a wide range of predators or only from salticids.

The most likely case is that the mimicry is directed solely toward jumping spiders. The behavior of salticids is often stereotyped and mediated by their highly developed visual system. Once an object is visually perceived, a jumping spider will advance in a predatory, agonistic, or courtship mode. If the fulgorid is perceived as another salticid the risk of predation is lessened, since jumping spiders often signal each other during interspecific and intraspecific encounters (Crane, 1949; Forster, 1982) and actual cannibalism or combat does not appear to be common (Crane, 1949).

Previous work supports the hypothesis that this mimicry is designed to deter only jumping spiders. Greene et al. (1987) found salticid mimicry by the tephritid *Z. vittigera* did not deter predation by nonsalticid spiders, mantids, assassin bugs, and whiptail lizards. Whitman et al. (1988) reported salticid mimicry by the same fly protected it from a number of sympatric salticid species. Jumping spiders perceived the flies as other jumping spiders and engaged in agonistic or courtship displays.

Using Vane-Wright's (1976) terminology, this case of a fulgorid mimicking salticids would be Class VI anteric defensive mimicry (Batesian). Here the model and operator (predator) would be the same. Since many species of jumping spiders and fulgorids occur in similar habitats, this type of mimicry may be more common than reported.

The only other apparent case of mimicry in fulgorids occurs in the lanternflies

(*Fulgoria* spp.). Hogue (1984) speculated they avoid predation by mimicking several genera of arboreal lizards.

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**BEMBIDION FEMORATUM STURM AND AMARA COMMUNIS  
(PANZER) (COLEOPTERA: CARABIDAE) NEW TO  
NORTH AMERICA**

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**Abstract.**—The Palaearctic species *Bembidion femoratum* Sturm and *Amara communis* (Panzer) are reported for the first time from North America. The first species is known from New Brunswick and Nova Scotia since 1967 and the second from New Brunswick since 1988. Both species were probably introduced through nursery stock. A short description and comments are provided for each species.

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From a practical point of view, introduced arthropods are important to mankind. Some are pests, others beneficial, and several could have an impact on local fauna by displacing native species or reducing their reproductive success. Early detection of exotic species has been advocated as a national priority in the U.S.A. (Hoebelke and Wheeler, 1983) and a computerized data base on immigrant arthropods has been recently developed (Knutson et al., 1990).

Recent collecting in The Maritimes has yielded two European carabids, *Bembidion femoratum* Sturm, 1825 and *Amara communis* (Panzer, 1797), previously not known to occur in North America. The purpose of this paper is to report the occurrence of these two species on this continent. A short description and comments are provided for each species to assist in their recognition.

*Bembidion femoratum* Sturm, 1825

**Description.** Body black, upper surface with faint metallic lustre; elytra with large humeral and apical rufous spots on each side, spots not linked laterally; apical spot usually extending to apex and suture; first antennomere and base of following 2 or 3 antennomeres pale, rufo-testaceous; penultimate maxillary and labial palpomeres and usually also preceding maxillary palpomere infuscated; femora infuscated, tibiae clearly paler than femora. Pronotum with sides less rounded than in *B. tetracolum*; basal punctures shallow, often confluent into longitudinal wrinkles; microsculpture weakly impressed laterally, absent on disc. Elytra parallel-sided; striae punctures smaller than in *B. tetracolum*; punctures of seventh stria distinctly smaller than those of sixth stria; microsculpture rather strong, markedly transverse, not forming distinct meshes. Aedeagus as illustrated (Fig. 1).

Length of body: 4.3–5.0 mm.

**Distribution.** This species occurs over most of Europe, from Scandinavia south to Spain and Italy (including Sicily), in Asia Minor, and in Siberia east to the Lena River (Lindroth, 1945); it was also reported from Mongolia (Poppius, 1907). In North America, this *Bembidion* is known from Cape Breton Island, continental Nova Scotia, and along the southern coast of New Brunswick. The first specimen collected

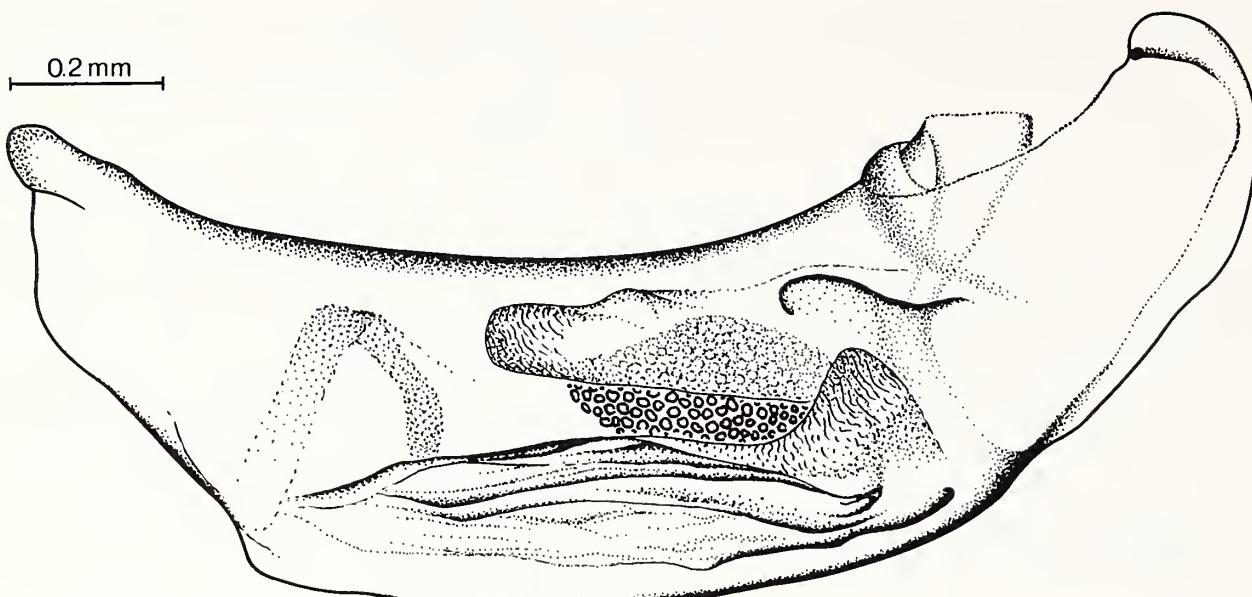


Fig. 1. Median lobe (left lateral view) of *Bembidion femoratum* (Sydney, Nova Scotia).

in the Nearctic Region was found in Lawrencetown near Halifax, Nova Scotia, on July 19–20, 1967. The specimen was identified by C. H. Lindroth in 1971.

**New Brunswick.** *St. John Co.*: St. John's, 7.VII.1988 (Larochelle & Larivière collection) 4.

**Nova Scotia.** *Halifax Co.*: Lawrencetown, 19–20.VII.1967 (Canadian National Collection) 1. *Cape Breton Co.*: Sydney, 12.VI.1983 (Canadian National Collection) 14.

**Habitat.** According to Lindroth (1985), the species occurs in Europe mainly near water, notably on river banks, on clay or clay-mixed sand, silt or gravel, often among sparse vegetation. It is also found, though less frequently, in gravel and clay pits, at roadsides and in cultivated fields, far from water. All North American specimens, except the one from Lawrencetown, were collected under rocks and debris on moderately moist, clayey soil in abandoned fields. At Sydney, it was found with several other European introduced carabids, including *B. tetricolum* Say.

**Wing Condition.** The wings are fully developed in this species and flight observations have been recorded (Lindroth, 1945).

**Discussion.** This *Bembidion* belongs to the *tetricolum* group as defined by Lindroth (1963:330–331). It differs from all other North American species of the group, except *B. petrosum attuense* Lindroth, 1963 and *B. poppii* Netolitzky, 1914, which occur in the Nearctic Region only in Alaska, by having the penultimate palpomeres, as well as the second and third antennomeres, infuscated at least apically, and no microsculpture on the disc of the pronotum.

To include this species in Lindroth's key (1963) to the Canadian and Alaskan species of *Bembidion*, the following changes should be made:

- 151. Pronotum with sides straight or very slightly sinuate toward base ... *B. nevadense* var.  
— Pronotum with sides distinctly sinuate toward base ..... 152
- 152. Seventh elytral stria with punctures as strong as those of sixth stria on basal half.  
[Alaska] ..... 152'

- Seventh elytral stria with punctures smaller than those of sixth stria on basal half.  
[Maritime Provinces] ..... *B. femoratum*
- 152'. Elytral spots poorly defined. Elytral microsculpture consisting of meshes on average less than twice as wide as long. Body length 4.9–5.9 mm ..... *B. petrosum attuense*
- Elytral spots well defined. Elytral microsculpture consisting of meshes more than twice as wide as long. Body length 3.8–4.4 mm ..... *B. poppii*

*Bembidion femoratum* is morphologically very similar to the European *B. andreae* (Fabricius) (cf. Lindroth, 1985) and has been considered as its subspecies by several authors.

### *Amara communis* (Panzer, 1797)

**Description.** Body black, upper surface brassy or occasionally greenish or bluish; first two antennomeres and base of third antennomere pale, yellowish, third antennomere infuscated on apical half; palpomeres, except basal ones, piceous to black; femora and tarsi rufopiceous to black, tibiae paler than femora. Head narrow with flat eyes. Pronotum with sides more or less rounded on basal half; anterior angles markedly, angularly produced; basal punctuation variable; basal foveae superficial, more or less distinct; posterior lateral seta on each side widely separated from lateral bead. Elytron with striae deepened apically; intervals more convex toward apex; setigerous punctures along eighth stria interrupted near middle; seventh stria with three subapical setae; parascutellar seta absent; microsculpture more or less isodiametric to slightly transverse, rather weakly impressed in male, well-impressed in female. Male hind tibia with setal brush on distal half of medial surface. Female with only two apical setae on last visible sternum. Aedeagus with apical lamella symmetrical, tapered; right paramere with marked hook.

Body length: 6.0–7.5 mm.

**Distribution.** This species occurs over most of Europe, from Scandinavia south to Spain and Italy, Asia Minor, the Caucasus, and across Siberia to the Kamchatka Peninsula (Lindroth, 1945). In North America, *A. communis* is known from two localities in southern New Brunswick.

**New Brunswick.** St. John Co.: West Quaco, 7.VII.1988 (Larochelle & Larivière collection) 2. Albert Co.: Waterside, 8.VII.1988 (Larochelle & Larivière collection) 6.

**Habitat.** According to Lindroth (1986), this eurytopic species is found on almost every kind of moderately dry soil in meadows, fields and woods, often under moss and dry leaves. The adults feed on plant seeds. The species is a spring breeder.

**Wing Condition.** The wings are fully developed and functional.

**Discussion.** *Amara communis* can be distinguished from all other North American species of *Amara* occurring in the northeast by the combination of having the first two antennomeres pale with the third one infuscated at apical half, the femora infuscated, no parascutellar seta, and the seventh elytral stria with three subapical setae.

To include this species in Lindroth's key (1966) to the Canadian and Alaskan species of *Amara*, the following changes should be made to couplets 51 and 54:

- |   |    |
|---|----|
| 51. Shoulder tooth obsolete. Seventh elytral stria with 2 subapical setae .....               | 52 |
| — Shoulder tooth often small but distinct. Seventh elytral stria with 3 subapical setae ..... | 53 |
| 54. Inner basal foveae of pronotum deep, linear and virtually parallel to median line ..      |    |

- ..... *A. aenea*
- Inner basal foveae of pronotum shallow, if linear then somewhat oblique ..... 54'
  - 54'. Elytral striae deepened toward apex, intervals more convex apically. Third antennomere infuscated in apical half ..... *A. communis*
  - Elytral striae shallow throughout, intervals quite flat. Third antennomere entirely pale or almost so ..... 55

This species is closely related to the European *A. convexior* Stephens. The latter differs by being more parallel-sided, by the more or less continuous setigerous punctures in the eighth stria and by the somewhat constricted apical lamella of the aedeagus (Lindroth, 1986).

#### DISCUSSION

With the addition of the two species herein reported, the fauna of northeastern North America now comprises 45 exotic carabid taxa (Table 1). In contrast, 21 introduced species are known from western North America, 15 being common to both sides of the continent (Spence, 1990).

Among the exotic carabids established in eastern North America, all but two were accidentally introduced. *Calosoma sycophanta* (Linné) and *Carabus auratus* Linné were intentionally introduced from Europe to Massachusetts in 1905–1910 for the control of the gypsy moth, *Lymantria dispar* (Linné) (Smith, 1959; Weseloh, 1986). Several other European species of *Carabus* and *Calosoma* were deliberately introduced into eastern North America but only the two above-mentioned species are established.

*Bembidion femoratum* and *Amara communis* are known in North America only from The Maritimes which probably represent the point of introduction. To be more specific, St. John, New Brunswick, could well be the port of entry for both species. Twenty-three species, about 50% of the exotic carabids found in northeastern North America, were first spotted on this continent in Newfoundland or The Maritimes. There is no doubt that ports in the Atlantic Provinces of Canada have been and are still the primary points of introduction of exotic species in northeastern North America. Other prime introduction areas in the northeast include ports along the Saint Lawrence, particularly Montreal (cf. *Blemus discus*, *Clivina fossor*), the Great Lakes region (cf. *Trechus quadristriatus*, *Bembidion obtusum*), and along the United States coast (cf. *Asaphidion flavipes*, *Clivina collaris*, *Harpalus puncticeps*, *Harpalus rubripes*).

Brown (1940) and Lindroth (1957) claimed that many introduced species in North America crossed the Atlantic with bulk rock and soil regularly taken aboard sailing vessels as ballast. As a rule, ballast was dumped ashore on the North American coast. Because this practice was abandoned after World War I (Lindroth, 1957) and the introductions of *B. femoratum* and *A. communis* are likely of recent origin, the presence of these two carabids in North America cannot be explained by this mode of introduction. So how did these species get here? Spence and Spence (1988), Kavanaugh and Erwin (1985), and Kelton (1983) considered it likely that European carabids and mirids were accidentally introduced to North America through nursery stock. I have no reason not to believe that the two species herein reported also could have been introduced with nursery stock.

Table 1. List of exotic carabid species likely established in northeastern North America.

Introduced species	Area of first record	Year of first record
<i>Abax parallelepipedus</i> (Piller & Mitterpacher)	Cape Breton, NS	1965
<i>Acupalpus meridianus</i> (Linné)	Quebec area, PQ	1969
<i>Agonum muelleri</i> (Herbst)	Newfoundland	<1840
<i>Amara aenea</i> (DeGeer)	?	<1828
<i>Amara apricaria</i> (Paykull)	?	<1875
<i>Amara aulica</i> (Panzer)	Cape Breton, NS	1929
<i>Amara bifrons</i> (Gyllenhal)	Cape Breton, NS	1929
<i>Amara communis</i> (Panzer)	New Brunswick	1988
<i>Amara eyrinota</i> (Panzer) <sup>1</sup>	Newfoundland	1971
<i>Amara familiaris</i> (Duftschmid)	Long Island, NY	1915
<i>Amara fulva</i> (Müller)	Newfoundland	1905
<i>Asaphidion flavipes</i> (Linné)	Long Island, NY	1930
<i>Bembidion bruxellense</i> Wesmael	Newfoundland	1907
<i>Bembidion femoratum</i> Sturm	Nova Scotia	1967
<i>Bembidion lampros</i> (Herbst)	Newfoundland	1949
<i>Bembidion obtusum</i> Audinet-Serville	Great Lakes area	1956
<i>Bembidion properans</i> (Stephens)	Nova Scotia	1947
<i>Bembidion stephensi</i> Crotch	Ottawa, ON	1891
<i>Bembidion tetracolum</i> Say	?	<1823
<i>Blemus discus</i> (Fabricius)	Montreal area, PQ	1933
<i>Broscus cephalotes</i> (Linné)	Cape Breton, NS/ Prince Edward Is.	1987
<i>Calosoma sycophanta</i> (Linné)	Massachusetts	1905–10
<i>Carabus auratus</i> Linné	Massachusetts	1908
<i>Carabus g. granulatus</i> Linné	Montreal, PQ	1952
<i>Carabus g. hibernicus</i> Lindroth	New Brunswick	1890
<i>Carabus nemoralis</i> Müller	New Brunswick	1870
<i>Clivina collaris</i> (Herbst)	Massachusetts	<1838
<i>Clivina fossor</i> (Linné)	Montreal area, PQ	1915
<i>Harpalus affinis</i> (Schrink)	?	<1798
<i>Harpalus puncticeps</i> (Stephens)	Long Island, NY	1954
<i>Harpalus rubripes</i> (Duftschmid)	New Hampshire	1981
<i>Harpalus rufibarbis</i> (Fabricius)	Montreal area, PQ	1953
<i>Harpalus rufipes</i> (DeGeer)	Prince Edward Is.	1937
<i>Laemostenus terricola</i> (Herbst)	Nova Scotia	<1894
<i>Leistus ferrugineus</i> (Linné)	Newfoundland	1977
<i>Notiophilus biguttatus</i> (Fabricius)	Newfoundland	1923
<i>Notiophilus palustris</i> (Duftschmid)	Nova Scotia	1967
<i>Paranchus albipes</i> (Fabricius)	Newfoundland	<1840
<i>Perigona nigriceps</i> (Dejean)	?	<1853
<i>Porotachys bisulcatus</i> (Nicolai)	? Massachusetts	<1900
<i>Pterostichus melanarius</i> (Illiger)	Nova Scotia	1926
<i>Pterostichus strenuus</i> (Panzer)	Newfoundland	1937
<i>Stomis pumicatus</i> (Panzer) <sup>2</sup>	Cape Breton, NS	1984
<i>Trechus quadristriatus</i> (Schrank)	Great Lakes area	1965
<i>Trechus rubens</i> (Fabricius)	Nova Scotia	<1875

<sup>1</sup> The name *eyrinota*, used by most authors for this taxon, is an incorrect subsequent spelling.<sup>2</sup> The first North American record of this species from Hemmingford in Quebec was based on a mislabelled specimen (cf. Bousquet, 1987:124).

To establish the source area of the two species herein reported is impossible. Lindroth (1957) argued that most European carabids introduced before World War I originated from England, particularly the southwestern region, because most of the transatlantic ballast traffic originated from that country. However, for *B. femoratum* and *A. communis* the best guess seems to be Holland. Both species are common in that country (Turin et al., 1977) and Holland has been by far the main source of nursery stock imported from Europe to Canada for at least the past 20 years (Duguay and Anderson, 1986).

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DESCRIPTIONS OF NEW OR POORLY KNOWN SPECIES  
OF *GASTROSTICTA* CASEY, 1918 AND  
*PARAFERONINA* BALL, 1965 (COLEOPTERA:  
CARABIDAE: *PTEROSTICHUS* BONELLI, 1810)

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*Abstract.*—Three new species of Pterostichini from North America are described: *Pterostichus enodis* (type locality: Texas), and *P. mutooides* (type locality: Georgia) which belong to the subgenus *Gastrosticta* Casey, 1918, and *P. spathifer* (type locality: Isabella Creek, Clearwater Co., Idaho) which is a member of the subgenus *Pseudoferonina* Ball, 1965. Three species of *Gastrosticta* are redescribed: *P. obesus* LeConte, 1873; *P. punctiventris* Chaudoir, 1878; and *P. ophryoderus* Chaudoir, 1878. *Pterostichus amnicola* (Casey, 1918) is listed as a new junior synonym of *P. punctiventris* (Chaudoir, 1878). A key to all known species of *Gastrosticta* is included.

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The purpose of this paper is to provide names for three undescribed species of *Pterostichus* Bonelli belonging to the subgenera *Gastrosticta* Casey and *Pseudoferonina* Ball and redescribe three species of *Gastrosticta* previously known only from the original descriptions. The new species are described herein so that the names could be used in a forthcoming publication dealing with the supraspecific classification of the North American Pterostichini. As members of *Gastrosticta* and *Pseudoferonina* are rare in collections, I hope this publication will stimulate anyone interested in North American Carabidae to collect and study these beetles.

Acronyms used in this publication are as follow: CAS—California Academy of Sciences, San Francisco, California; CMNH—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CNC—Canadian National Collection, Ottawa, Ontario; MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts; MNHP—Muséum National d'Histoire Naturelle, Paris; UASM—University of Alberta Strickland Museum, Edmonton, Alberta; UICM—Department of Plant, Soil & Entomological Sciences, University of Idaho, Moscow, Idaho; USNM—United States National Museum (Natural History), Washington, DC.

Subgenus *Gastrosticta* Casey, 1918

*Gastrosticta* Casey, 1918:323. Type species: *Feronia ventralis* Say, 1823, by original designation.

*Gastrosticta* is one of the most poorly known North American subgenera of *Pterostichus*. It includes ten species: *P. ventralis* (Say, 1823); *P. putus* Casey, 1913; *P. sayanus* Csiki, 1930 [replacement name for *P. obscurus* (Say, 1834)]; *P. subacutus* (Casey, 1918); *P. tumescens* LeConte, 1863; *P. obesus* LeConte, 1873; *P. punctiventris* (Chaudoir, 1878); *P. ophryoderus* (Chaudoir, 1878); and the two species described in this paper. The group is restricted to the temperate regions of eastern United States.

According to Ball (1960) members of this subgenus live in dry, open, coniferous woodlands; all species are brachypterous.

Adults of *Gastrosticta* are distinguished from those of other North American Pterostichini by the laterally punctate sterna in combination with the absence of scutellar stria, lack of seta on the hind trochanter, glabrous last tarsomere, and poorly developed metatarsal carina. All these character states are apotypic within the Pterostichini; likely *Gastrosticta* is a monophyletic taxon.

Three species of this group, *P. obesulus*, *P. punctiventris*, and *P. ophryoderus*, are known only from the original descriptions which are difficult to interpret. These species are redescribed herein along with two new species; a key to the species of the subgenus is also provided.

*Pterostichus obesulus* LeConte, 1873

*Pterostichus obesulus* LeConte, 1873:314. Type locality: Georgia.

**Diagnosis.** Unique among the species of *Gastrosticta* by the characteristic shape of the pronotum (Fig. 2) with the lateral depressions explanate basally.

**Description.** **Habitus** (Fig. 1). **Coloration.** Body rufopiceous to piceous dorsally; antennae, palpi, legs, lateral margins of pronotum and sometimes first elytral intervals testaceous to dark ferruginous; elytra iridescent. **Microsculpture.** Frons with poorly impressed, isodiametric meshes. Pronotum with very transverse meshes. Elytra with linear microsculpture (i.e., meshes linear, narrow, parallel, with few anastomoses). **Head.** Frontal impressions shallow, more or less parallel, impunctate. **Pronotum** (Fig. 2). Widest around middle; sides rounded on posterior half; posterior angles rounded; lateral bead thickened basally; lateral depression explanate basally; base not or faintly and partly marginated laterally; laterobasal impression single, short, shallow, punctate; area between laterobasal impression and lateral margin depressed. **Elytra.** Moderately long (index length elytra/length pronotum = 2.06–2.28); sixth and seventh striae not impressed, at most suggested; striae punctate, except on apical fourth and sometimes also on basal fourth; intervals convex; second discal setigerous puncture on or near second stria. **Legs.** Apical spur of fore tibia markedly dilated laterally. **Ventral parts.** Proepisternum without punctures. Metepisternum punctate. Sternum VII with punctures medially, punctuation as dense as on lateral areas. **Aedeagus.** Median lobe with short apex, apical lamella rounded (Fig. 8); right paramere elongate, markedly curved apically (Fig. 8).

Length of body: 8.1–9.5 mm.

**Type material.** LeConte's collection in MCZ includes a single specimen under the name of *P. obesulus*. The specimen, a female, bears the following labels: "Ga/ Horn Coll H554/ *P. obesulus* LeC/ Lectotype MCZ 32326/ Designated 1975 R.T.Allen/ UAIC 00015001." LeConte's original description was based on a single specimen since he wrote (1873:314) "I have seen only the specimen kindly communicated by Dr. Horn." The specimen therefore is the holotype (by monotypy).

**Distribution.** The species is known from Georgia, Florida, and Louisiana. In addition to the holotype, I have seen five specimens of this species from the following localities. **Florida:** "Fla", Liebeck (MCZ) 1; Alachua Co., Gainesville, 29.I.1972, D. R. Whitehead (UASM) 1; idem, 9–17.IV.1986, G. Gibson (CNC) 1; boundary of

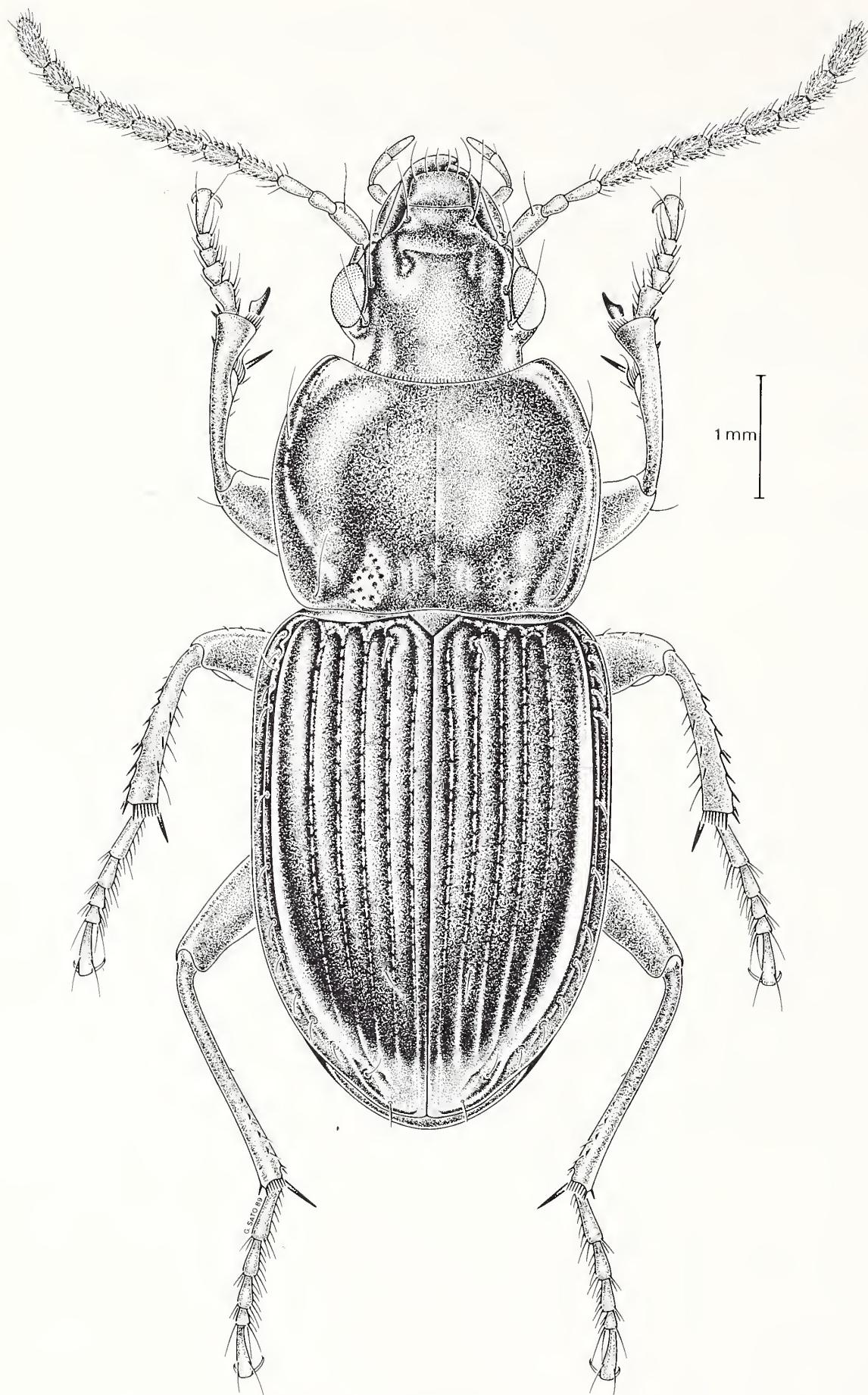
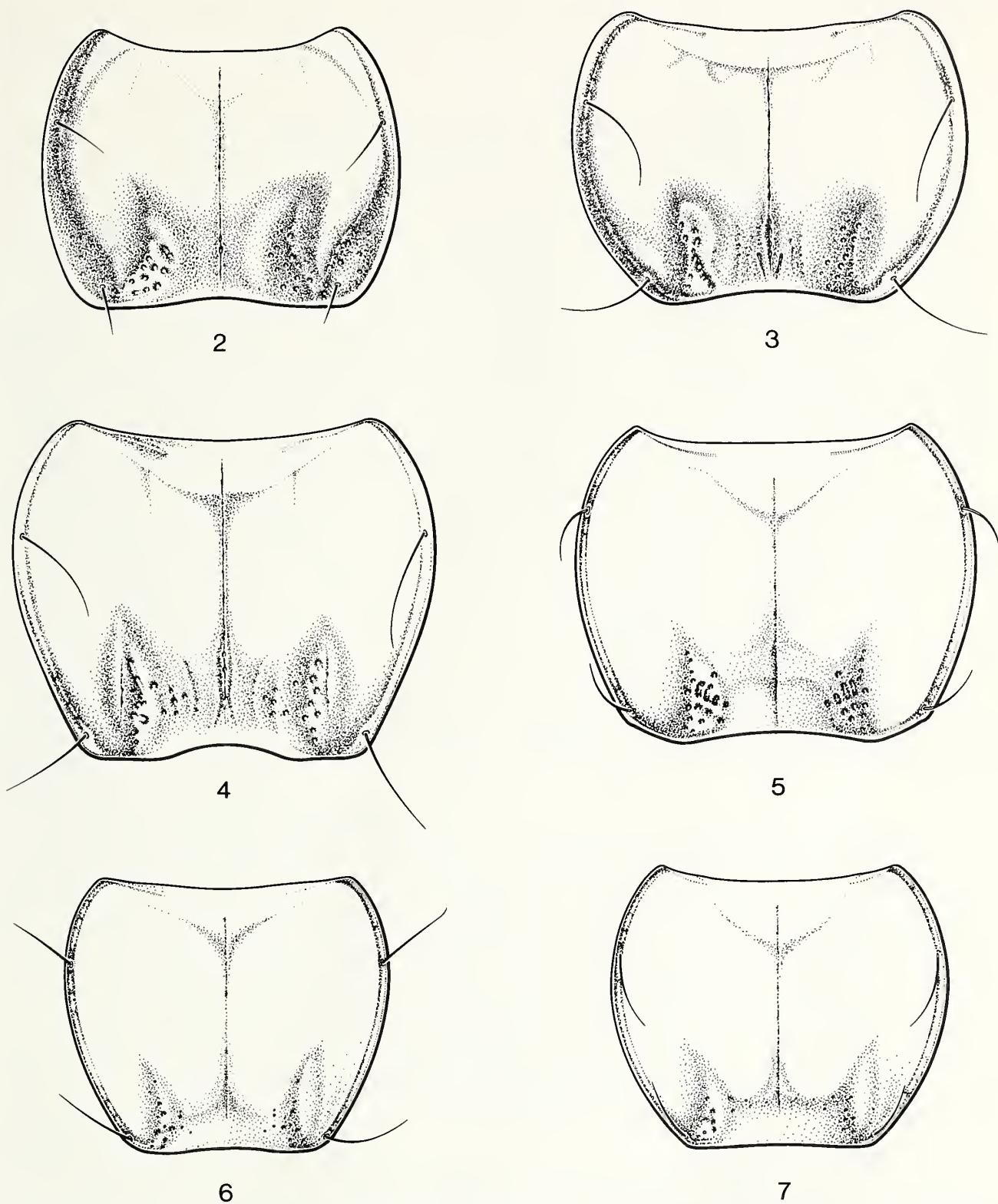


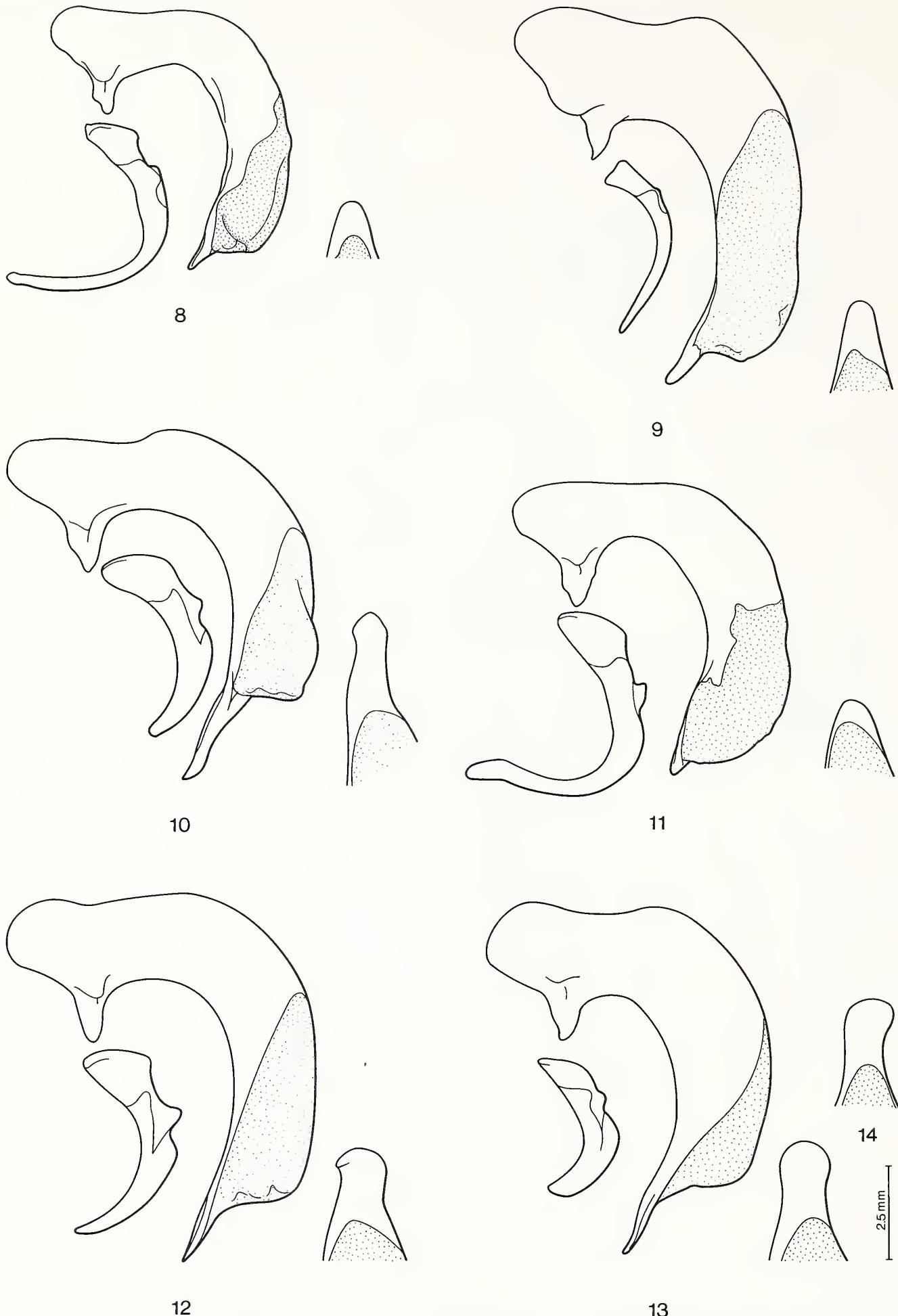
Fig. 1. *Pterostichus obesulus* LeConte, female.



Figs. 2–7. Pronotum. 2. *Pterostichus obesulus*; 3. *P. ophryoderus* (lectotype); 4. *P. punctiventris* (lectotype); 5. *P. mutoides* (paratype); 6. *P. ventralis*; 7. *P. putus* (lectotype).

Levi-Alachua Co., 14–16.IV.1986, G. Gibson (CNC) 1. Louisiana: "La", Liebeck (MCZ) 1.

**Comments.** LeConte (1873:307) originally included *P. obesulus* in his section D of the genus *Pterostichus* along with *P. fallax* (Dejean, 1828) and *P. sculptus* LeConte, 1852. Lindroth (1966:535) did not study any specimens of *P. obesulus* and, following LeConte, included the species in *Abacidus* LeConte, a group that contains both *P.*



Figs. 8–14. Median lobe (left lateral view), right paramere, and apical lamella. 8. *Pterostichus obesus* (Gainesville, Florida); 9. *P. ophryoderus* (5 mi S. Toomsuba, Mississippi); 10. *P. sayanus* (Charleston, Illinois); 11. *P. enodis* (holotype); 12. *P. mutoides* (holotype); 13. *P. ventralis* (neotype); 14. Apical lamella of median lobe of *P. putus* (lectotype).

*fallax* and *P. sculptus*. The species, however, without doubt belongs to the subgenus *Gastrosticta*.

*Pterostichus ophryoderus* (Chaudoir, 1878)

*Feronia ophryodera* Chaudoir, 1878:64. Type locality: Mississippi.

**Diagnosis.** Distinguished from the other *Gastrosticta* by the characteristic shape of the pronotum (Fig. 3) with the wide lateral depressions.

**Description. Coloration.** Body ferruginous with antennae, palpi, legs, sides of pronotum and elytra fulvous. **Microsculpture.** Frons without distinct microsculpture. Pronotum and elytra with linear microsculpture. **Head.** Frontal impressions shallow, more or less parallel, impunctate. **Pronotum** (Fig. 3). Widest in front of middle; sides rounded on posterior half, more constricted than in *P. obesus*; posterior angles rounded; lateral bead regular; lateral depression rather wide, not explanate basally; base laterally marginate; laterobasal impression shallow, barely punctate; area between laterobasal impression and margin convex. **Elytra.** Proportionally long (index length elytra/length pronotum = 2.54); sixth and seventh striae not impressed, at most suggested; striae punctate, except on apical fourth and sometimes also on basal fourth; intervals slightly convex; second discal setigerous puncture situated on or near third stria. **Legs.** Apical spur of fore tibia feebly dilated laterally. **Ventral parts.** Proepisternum and metepisternum smooth. Sternum VII with few punctures restricted to anterolateral areas. **Aedeagus.** Median lobe with moderately long apex, apical lamella rounded (Fig. 9); right paramere elongate, slightly curved apically (Fig. 9).

Length of body: 9.7–10.2 mm.

**Type material.** Chaudoir's collection in MHNP contains a single specimen, a female, under this name labelled: ““Mississippi” Sallé (handwritten)/Holotype/ *Feronia ophryodera* Chaud. Holotype (handwritten)/ Muséum Paris 1952 Coll R Oberthur.” It is obvious that these labels are not the original ones. The specimen, however, agrees with Chaudoir's description and I have no doubt that it is part of the type series. Chaudoir did not mention the number of specimens in the original series and, since he did not properly label his type material (Ball and Erwin, 1983), the specimen can not be regarded as the holotype. The specimen is herein selected as lectotype and the label “Lectotype *Feronia ophryodera* Chaudoir Des. by Y. Bousquet 1989” has been attached to it.

**Distribution.** In addition to the lectotype, I have seen one male and one female of this species from the following localities. **Mississippi:** Lauderdale Co., 5 mi S Toomsburg, U.S. 11, 14.VI.1965, R. Freitag & D. Larson (CNC) 1; Rankin Co., Flowood, 28.II.1988, D. & M. Hildebrandt (Hildebrandt Coll.) 1 [cypress swamp on banks of Pearl River].

*Pterostichus punctiventris* (Chaudoir, 1878)

*Feronia punctiventris* Chaudoir, 1878:66. Type locality: Texas.

*Gastrosticta amnicola* Casey, 1918:372 (New Synonymy). Type locality: St. Louis, Missouri.

**Diagnosis.** Distinguished by the combination of having the sides of the pronotum obliquely convergent in posterior half, the elytral microsculpture transverse, and the second discal seta in or close to second stria.

**Description. Coloration.** Body ferruginous with antennae and palpi fulvous; tibiae darker than femora. **Microsculpture.** Frons with poorly impressed, isodiametric meshes. Pronotum and elytra with transverse meshes. **Head.** Eyes less convex than in *P. obesus*. Frontal impressions shallow, more or less parallel, impunctate. **Pronotum** (Fig. 4). Widest in front of middle; sides obliquely convergent on posterior half; posterior angles obtuse; lateral bead regular; lateral depression not explanate basally; base marginated laterally; laterobasal impression slightly longer, deeper and more punctate than in *P. obesus*; area between laterobasal impression and margin convex. **Elytra.** Proportionally long (index length elytra/length pronotum = 2.42–2.48); sixth and seventh striae feebly impressed on anterior half, more so on posterior half; striae punctate, except on apical fourth and sometimes also on basal fourth; intervals slightly convex; second discal setigerous puncture situated on or near second stria. **Legs.** Apical spur of fore tibia feebly dilated laterally. **Ventral parts.** Proepisternum impunctate or with few punctures anteriorly. Metepisternum punctate. Sternum VII smooth medially or with few punctures, punctuation if present much sparser than on lateral areas. **Aedeagus.** Apical lamella rounded apically much like that of *P. ventralis* (cf. Fig. 13); right paramere more or less elongate, slightly curved apically (as in Fig. 12).

Length of body: 9.7–10.2 mm.

**Type material.** Chaudoir's collection in MHNP contains a single specimen under this name, a female labelled: ““Texas” Schmelb. (handwritten)/ Holotype/ *Feronia punctiventris* Chaud. Holotype (handwritten)/ Muséum Paris 1952 Coll R Oberthur.” As for the preceding species, it is obvious that these labels are not the original ones. The specimen, however, agrees with Chaudoir's description and I have no doubt that it is part of the type series. It is selected herein as lectotype and the label “Lectotype *Feronia punctiventris* Chaudoir Des. by Y. Bousquet 1989” has been attached to it.

Casey's collection in USNM contains two specimens under the name *Gastrosticta amnicola*. One of them, a male labelled “MO./ *Gastrosticta amnicola* Csny (handwritten)/ Type USNM 47116/ Casey bequest 1925/ UAIC 00044070/ Lectotype *Gastrosticta amnicola* [sic!] by (handwritten) R. T. Allen,” was selected lectotype by Allen (1977).

**Distribution.** In addition to the type material, I have seen 2 specimens of this species in the CNC. **Arkansas.** Stone Co., Blanchard Springs St. Park, 18.V.1973, Kavanaugh & Goulet. **Missouri.** St. Louis Co., Ranken, 4.X.36, E. P. Meiners.

**Comments.** I have found no external character states to distinguish the type specimens of *P. amnicola* (Casey) from the lectotype of *P. punctiventris* (Chaudoir). Therefore, *Gastrosticta amnicola* Casey, 1918 is herein considered as a junior synonym of *Feronia punctiventris* Chaudoir, 1878.

#### *Pterostichus enodis*, new species

**Diagnosis.** Distinguished from other species of *Gastrosticta* by the rather well impressed sixth and seventh elytral striae.

**Description. Coloration.** Body black with antennae, palpi, and legs rufopiceous. **Microsculpture.** Frons without distinct microsculpture. Pronotum and elytra with linear microsculpture. **Head.** Frontal impressions deeper than on preceding species, more or less parallel, punctate. **Pronotum.** Widest at middle; sides rounded on posterior half; posterior angles rounded; lateral depression not explanate basally; laterobasal impression short, shallow, faintly punctate; area between laterobasal impression and lateral margin convex. **Elytra.** Moderately long (index length elytra/length pronotum = 2.18); sixth and seventh striae impressed, as much as, or nearly as, fifth stria; striae punctate in basal half; intervals convex; second discal setigerous puncture on or near second stria. **Legs.** Apical spur of fore tibia markedly dilated laterally. **Ventral parts.** Proepisternum punctate on anterior half; metepisternum impunctate. **Aedeagus.** Median lobe with short apex, apical lamella rather rounded (Fig. 11); right paramere markedly curved apically (Fig. 11).

Length of body: 10.8 mm.

**Type material.** Holotype. Texas: "Tex/ Henry Ulke Beetle Coll. CMNH Acc. No. 1645/ Holotype *Pterostichus enodis* Bousquet." The specimen is deposited in the CMNH.

The specimen, a male, has lost the last 2 left antennomeres, the last 2 left labial palpomeres, the right maxillary palpus, the tibia and tarsus of the right front, left middle and right hind legs, and the tarsus of the right middle and left hind legs.

**Distribution.** The species is known only from the holotype collected in Texas.

**Etymology.** The specific name is derived from the Latin adjective *enodis*, *e* (without knots, smooth). It refers to the fact that the integument of the species is smooth and polished, the microsculpture on the pronotum and elytra being of the linear type.

**Comments.** The shape of the median lobe and particularly the markedly curved apical half of the right paramere suggest that this species and *P. obesus* are probably sister species.

#### ***Pterostichus mutoides*, new species**

**Diagnosis.** Separated from the other *Gastrosticta* by the characteristic shapes of the pronotum (Fig. 5) and of the median lobe (Fig. 12).

**Description. Coloration.** Body ferruginous with antennae, palpi, epipleura, tibiae, and tarsi flavous. **Microsculpture.** Frons without distinct microsculpture. Pronotum with very transverse meshes, meshes poorly impressed and distinct only by spots. Elytra with transverse meshes. **Head.** Frontal impressions shallow, more or less parallel, impunctate. **Pronotum** (Fig. 5). Widest in front of middle; sides straightly convergent on posterior half; posterior angles markedly obtuse; lateral bead regular; lateral depression not explanate basally; laterobasal impression short, shallow, punctate; area between laterobasal impression and lateral margin convex. **Elytra.** Proportionally long (index length elytra/length pronotum = 2.40); sixth and seventh striae feebly impressed; striae impunctate; intervals slightly convex; second discal setigerous puncture on or near second stria. **Legs.** Apical spur of fore tibia feebly dilated laterally. **Ventral parts.** Proepisternum impunctate. Metepisternum with few punctures. Sternum VII with punctuation restricted to anterolateral areas. **Aedeagus.** Median lobe with moderately long apex, apical lamella with minute jag (Fig. 12); right paramere more or less elongate, slightly curved apically (Fig. 12).

Length of body: 9.6–10.0 mm.

**Type material.** Holotype. Georgia: "Ga./ Holotype *Pterostichus mutoides* Bousquet." The specimen lacks the tarsus of the right middle leg.

One paratype labelled "Ga/ Paratype *Pterostichus mutoides* Bousquet." The holotype is deposited in the CMNH, the paratype in the CNC.

**Distribution.** The species is known only from the type material collected in Georgia.

**Etymology.** The specific name is derived from the specific name *mutus* and the suffix *oides* (like, resembling); it refers to the fact that the adults superficially look like those of *P. mutus*, a species of the subgenus *Bothriopterus* Chaudoir.

#### KEY TO SPECIES OF *GASTROSTICTA*

The key is preliminary and is given to facilitate the interpretation of the species described above.

1. Frontal impressions deep, grooved, distinctly divergent posteriorly. Laterobasal impressions of pronotum deep, convergent posteriorly ..... 2
- Frontal impressions superficial, not grooved, more or less parallel in most species; if moderately deep and slightly divergent posteriorly, then laterobasal impressions of pronotum superficial and more or less parallel ..... 3
- 2(1). Sides of pronotum rounded on posterior half; posterior angles minutely denticulate ..... *P. subacutus* (Casey)
- Sides of pronotum straightly convergent on posterior half; posterior angles obtuse ..... *P. tumescens* LeConte
- 3(1). Second discal puncture of elytron in or close to third stria ..... 4
- Second discal puncture of elytron in or close to second stria ..... 5
- 4(3). Elytral striae smooth. Microsculpture on elytra slightly transverse. Apical lamella of median lobe rather long, more or less triangular apically (Fig. 10) ..... *P. sayanus* Csiki
- Elytral striae punctate, punctures rather small and sparse but distinct. Microsculpture on elytra linear. Apical lamella of median lobe rather short, rounded apically (Fig. 9) ..... *P. ophryoderus* (Chaudoir)
- 5(3). Sixth and seventh striae clearly impressed in basal half, as much, or nearly so, as fifth stria ..... *P. enodis*, new species
- Sixth and especially seventh striae indistinct, or much less impressed in basal half than fifth stria ..... 6
- 6(5). Lateral depression of pronotum explanate basally (Fig. 2); base of pronotum not or faintly and partly marginate laterad of laterobasal impression. Right paramere markedly curved in apical half (Fig. 8) ..... *P. obesus* LeConte
- Lateral depression of pronotum regular, not explanate basally (Figs. 4–7); base entirely and distinctly marginate laterad of laterobasal impression. Right paramere at most slightly curved in apical half (Figs. 12–13) ..... 7
- 7(6). Elytra without microsculpture, except on apical fourth. Last visible sternite with punctures medially, punctuation as dense as that on lateral areas ..... 8
- Elytra with microsculpture all over. Last visible sternite with very few punctures medially or without punctures, punctuation if present much sparser than that on lateral areas ..... 9
- 8(7). Pronotum markedly constricted basally (Fig. 6); greatest width at or near level of anterolateral seta. Apical lamella of median lobe with rounded apex (Fig. 13) ..... *P. ventralis* (Say)
- Pronotum less constricted basally (Fig. 7); greatest width behind level of anterolateral seta. Apical lamella of median lobe slightly distorted to right (Fig. 14) .. *P. putus* Casey

- 9(7). Pronotum with sides regularly rounded in posterior half (Fig. 5); basal margin extending medially beyond level of laterobasal impression ..... *P. mutoides*, new species
- Pronotum with sides rather obliquely convergent in posterior half (Fig. 4); basal margin not extending medially beyond level of laterobasal impression .....  
..... *P. punctiventris* (Chaudoir)

Subgenus *Pseudoferonina* Ball, 1965

*Pseudoferonina* Ball, 1965:107. Type species: *Pterostichus lanei* Van Dyke, 1925, by original designation.

Members of the subgenus *Pseudoferonina* are known only from the states of Idaho, Oregon, and Washington. Six species have been described: *P. vexatus* Bousquet, 1985; *P. shulli* (Hatch, 1949); *P. lanei* Van Dyke, 1925; *P. humidulus* (Van Dyke, 1943); *P. smetanai* Bousquet, 1985; and *P. campbelli* Bousquet, 1985. A key to these species was published recently (Bousquet, 1985); a new species from Idaho is described herein.

***Pterostichus spathifer*, new species**

**Diagnosis.** Adults of this species are externally similar to those of *P. shulli* and can be differentiated only by the examination of the median lobe of the aedeagus (see Figs. 15–16). In *P. spathifer* the median swelling on the left side of the median lobe is less rounded, the submedian sinuosity is slightly more anterad, and the apex is wide, spoonlike, and slightly distorted to the right.

**Description. Coloration.** Dorsal surface of body black; antennae and legs rufous to rufopiceous; palpi usually rufous. **Microsculpture.** Frons with isodiametric meshes. Pronotum and elytra with moderately transverse meshes. **Pronotum.** Sides oblique to sinuate in posterior half; anterior angles markedly produced; posterior angles right to obtuse; outer laterobasal impressions slightly to distinctly impressed; inner laterobasal impressions punctate. **Legs.** Mesotibia of male slightly curved apically. **Ventral parts.** Sternum VII of male with shallow, medial depression more or less delimited anteriorly by arcuate carina. **Aedeagus** (Fig. 15). Left side of apical portion of median lobe (in left lateral view) sinuate submedially; apex of median lobe (in left lateral view) wide, spoonlike; apical portion of median lobe (in ventral view) with lightly sclerotized diagonal band.

Length of body: 10.0–10.8 mm.

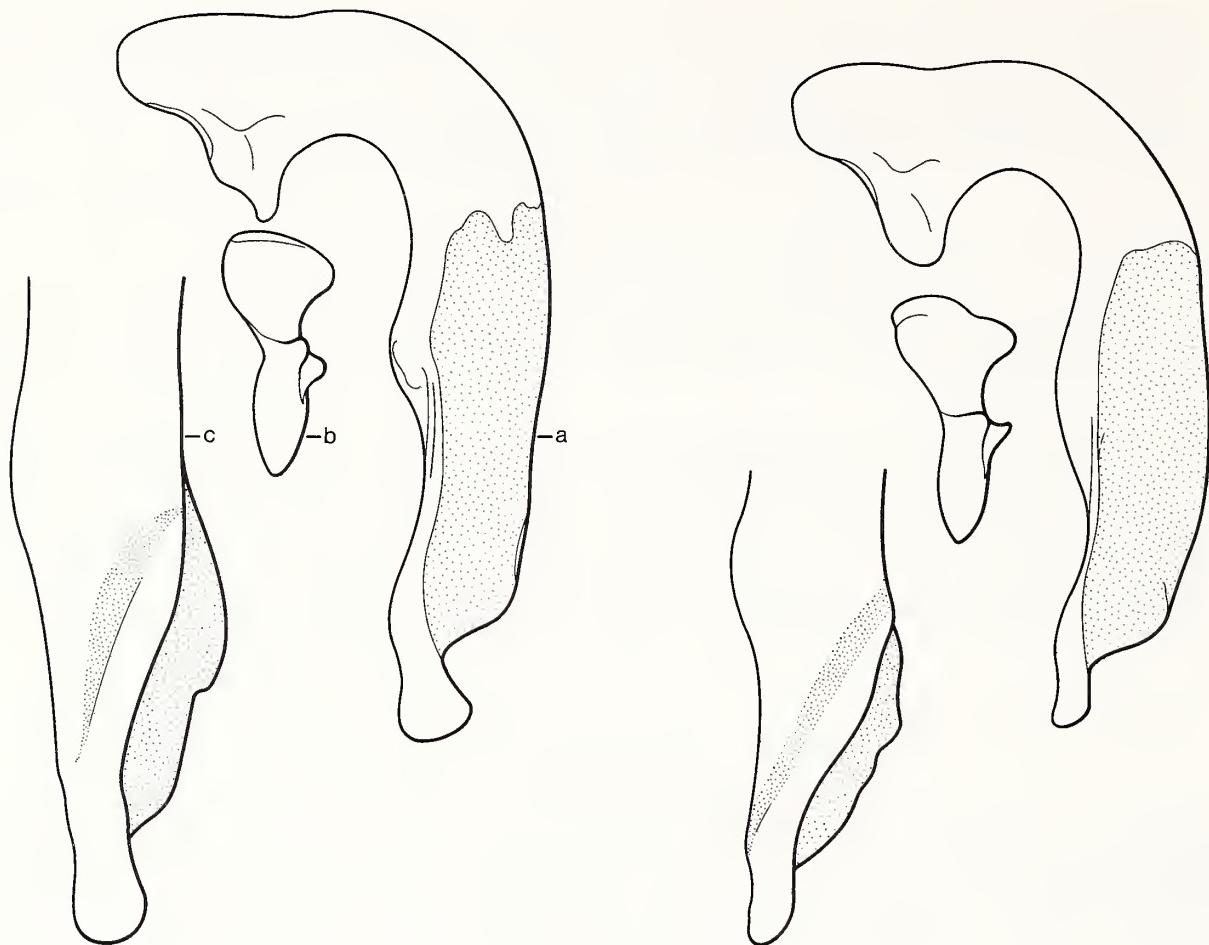
**Type material.** Holotype (male). Idaho: "Idaho, Clearwater Co. Isabella Creek, 1,700', S31, T41N, R7E, nr N.Fk. Clearwater River, 17.IX.1984, P. J. Johnson, J. B. Johnson." The specimen is deposited in the CAS.

Paratypes. Idaho: same data as holotype (8 males, 9 females), or date 24.VI.1985 (8 males, 8 females). The specimens are deposited in the CNC (10 specimens), USNM (5), CAS (7), UICM (6) and P.J. Johnson's collection (5).

**Distribution.** The species is known only from the type-locality in Idaho.

**Habitat.** All specimens were collected under alluvial cobbles partly imbedded in sand and partly covered with moss in a seasonally mostly dry side channel of Isabella Creek (P. Johnson, pers. comm.).

**Etymology.** The specific name is derived from the Latin noun *spatha*, -ae, f (spoon)



15

16

Figs. 15–16. Median lobe (left lateral view), right paramere, and apical half of median lobe (ventral view). 15. *P. spathifer* (holotype); 16. *P. shulli* (holotype).

and the verb *ferre* (to bear). It refers to the spoonlike apex of the median lobe in left lateral view.

**Comments.** To include the new species in Bousquet's key (1985), the following changes should be made.

- 3. Median lobe of aedeagus in left lateral aspect strongly sinuate behind middle ..... 3'
- Median lobe of aedeagus in left lateral aspect not sinuate behind middle .....  
..... *P. lanei* Van Dyke
- 3'. Median lobe of aedeagus with apex wide, spoonlike, and slightly distorted to right in left lateral aspect (Fig. 15) ..... *P. spathifer*, new species
- Median lobe of aedeagus with apex narrower, not spoonlike, and rather straight in left lateral aspect (Fig. 16) ..... *P. shulli* (Hatch)

#### ACKNOWLEDGMENTS

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## A HIGH ANDEAN NEW SPECIES OF *TERRA* (LEPIDOPTERA, LYCAENIDAE)

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*Abstract.*—*Terra altilineata*, new species, is described from a small spring-fed oasis isolated in high montane arid terrain (3,500–3,650 m), Jujuy Province, Argentina. Several other undescribed butterflies are endemic to this site.

I recently revised the Neotropical hairstreak butterfly genera *Nesiostrymon* Clench and *Terra* Johnson and Matusik (Theclinae, Eumaeini) (Johnson, 1991a). Both genera occur throughout the mainland neotropics and in the Greater Antilles and, as revised, included five and six respective species. Neither genus contained a high Andean representative, though *Nesiostrymon australivaga* Johnson was described from low latitude scrub-steppe in Mendoza Province, Argentina. Subsequently, a new species of *Terra* was collected in isolated high montane habitat, Jujuy Province, Argentina, at altitudes over 2,000 meters higher than any previously known congener. This distinctive new species is described below, following on the generic diagnosis of Johnson and Matusik (1988) and Johnson (1991a).

### ***Terra altilineata*, new species** Figs. 1A, 2B

**Diagnosis.** Hindwing under surface with thin lineal black medial band (congener exhibit lunulate yellow, or wide lineal red or yellow-brown, medial bands); male forewing upper surface with narrowly elliptic black androconial “brand” (*sensu* Eliot, 1973) contrasting lighter brown apical wing color (lowland Argentina congener *T. cana* (Hayward) with black wing apices in both sexes, obscuring dark ovate androconial brand in males). Valvae of male genitalia with distinctive lateral shoulders.

**Description.** *Male.* Upper Surface of Wings: ground color of both wings dusted light silvery blue; forewing with brown apices contrasted by black elliptic brand at distal end of discal cell; hindwing with thin white line along margin, adjacent hairlike tails at termini of veins CuA1 and CuA2. Under Surface of Wings: ground color of both wings concolorous gray; forewing with dull gray lineal band across postmedial area; hindwing with thin, undulate, black band across medial area; limbal area with small black marginal spot in cell CuA1. Length of forewing: 11.0–12.5 mm. *Female.* Unknown. *Male Genitalia.* Figure 2B (congener, Johnson, 1991a, figs. 59, 69–80, and as noted below). Terminal tergites typical of genus but brush organs uniquely absent. Genitalia with vinculum typical of genus but saccus stouter, terminus flattened; aedeagus elongate as in congeners but with heavily sclerotized, basally prong-like, terminus; valvae shouldered with distinctively elliptic sclerotized elements (Fig. 2, B5y), each bordered inwardly by slight ventral ridge extending caudally beneath the terminal microtrichia otherwise characteristic of the genus (Fig. 2, A1x; B3x).

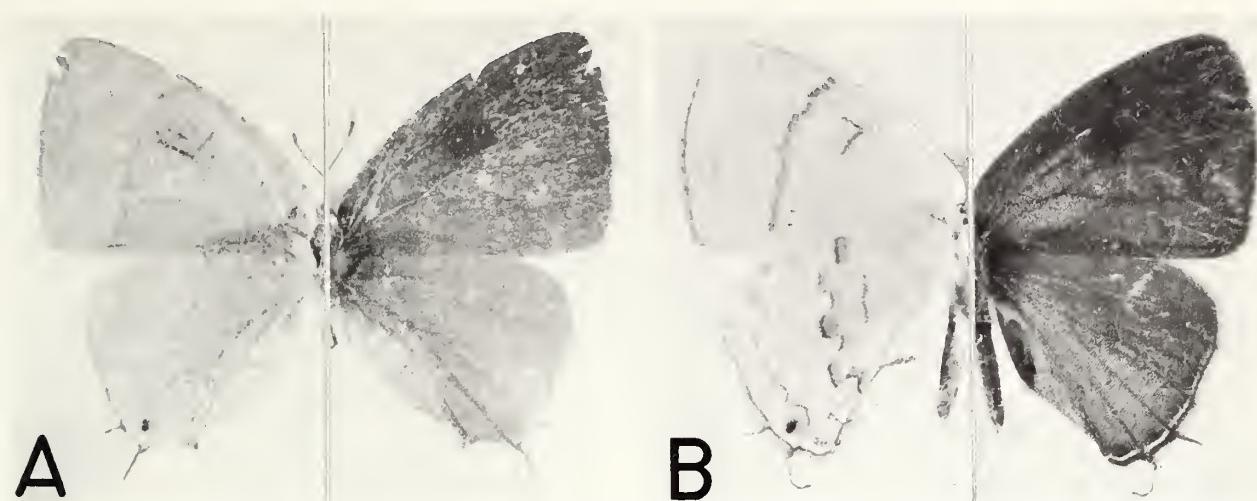


Fig. 1. Adults of *Terra altilineata* (A): holotype, upper surface right, under surface left; and *T. cana* (B): same aspects, male (Tucumán Prov, Dept. Yerba Buena, Rte. 338, km post 15, Cumbres San Javier, 700 m, 8 February 1991), AMNH.

**Types.** Holotype male (forewing 11.0 mm) (Fig. 1A), Quebrada de las Cruces, Dept. Tilcara, Jujuy Province, Argentina, 3,500 m, 1,130 hr, February 2, 1991, in boulder-strewn, dry wash some 100 m south of small spring-fed oasis (see Remarks); deposited American Museum of Natural History (AMNH). Paratypes. Same data as holotype, two males deposited Instituto Miguel Lillo, Tucumán, Argentina.

**Distribution.** Currently known only from type locality (see Remarks).

**Remarks. Habitat.** — *T. altilineata* is currently known from a boulder-strewn dry wash approximately 100 m south of a long, narrow, spring-fed oasis within “Quebrada de las Cruces” (found on most Jujuy Province topographic maps about 5 km W of Huacalera village [2,700 m, see site description 53A, Johnson et al., 1990]). On the sampling date, extent of oasis vegetation was approximately 2 km by 30 m along spring-fed rivulets extending from 3,500–3,650 m altitude, km 8–10, of the “Abra de las Cruces” footpath (known to most local residents and originating from the road leading south from the east end of Huacalera’s Rio Grande River bridge). The larval foodplant of *T. altilineata* probably occurs in the oasis; however, the type specimens were collected in the adjacent unvegetated wash. Other butterflies were observed some 100–200 m from the oasis, including various Lycaenidae (Theclinae, Polyommatinae) and Hesperiidae “mud-puddling” at rivulets up to 100 m north of the dry arroyo bed. In certain years, small spring- and snow-fed lakes or marshes occur about 5 km north and upland from the oasis (the “Lagunas de las Cruces” of most maps, 4,250 m). Thus, more extensive vegetation apparently occurs at certain times along the quebrada footpath upland of 3,500 m. In 1991 the “lagunas” were dry; aside from occasional upland xerophiles of the Pieridae and Satyridae, few butterflies were observed there. Robert C. Eisele (Jujuy, Argentina, pers. comm.) reports the 1991 sampling at Quebrada de las Cruces as the second known visit there by lepidopterists. To date, three other undescribed species of butterflies, two Lycaenidae and one Satyridae (all of uncertain generic assignment) are known only from this isolated locality. Johnson (1992) placed one new thecline from the oasis in a new genus (*Shapiroana matusikorum*). It is the southernmost member of a group occurring at very high altitudes north to the Sierra Nevada de Santa Marta of Colombia.

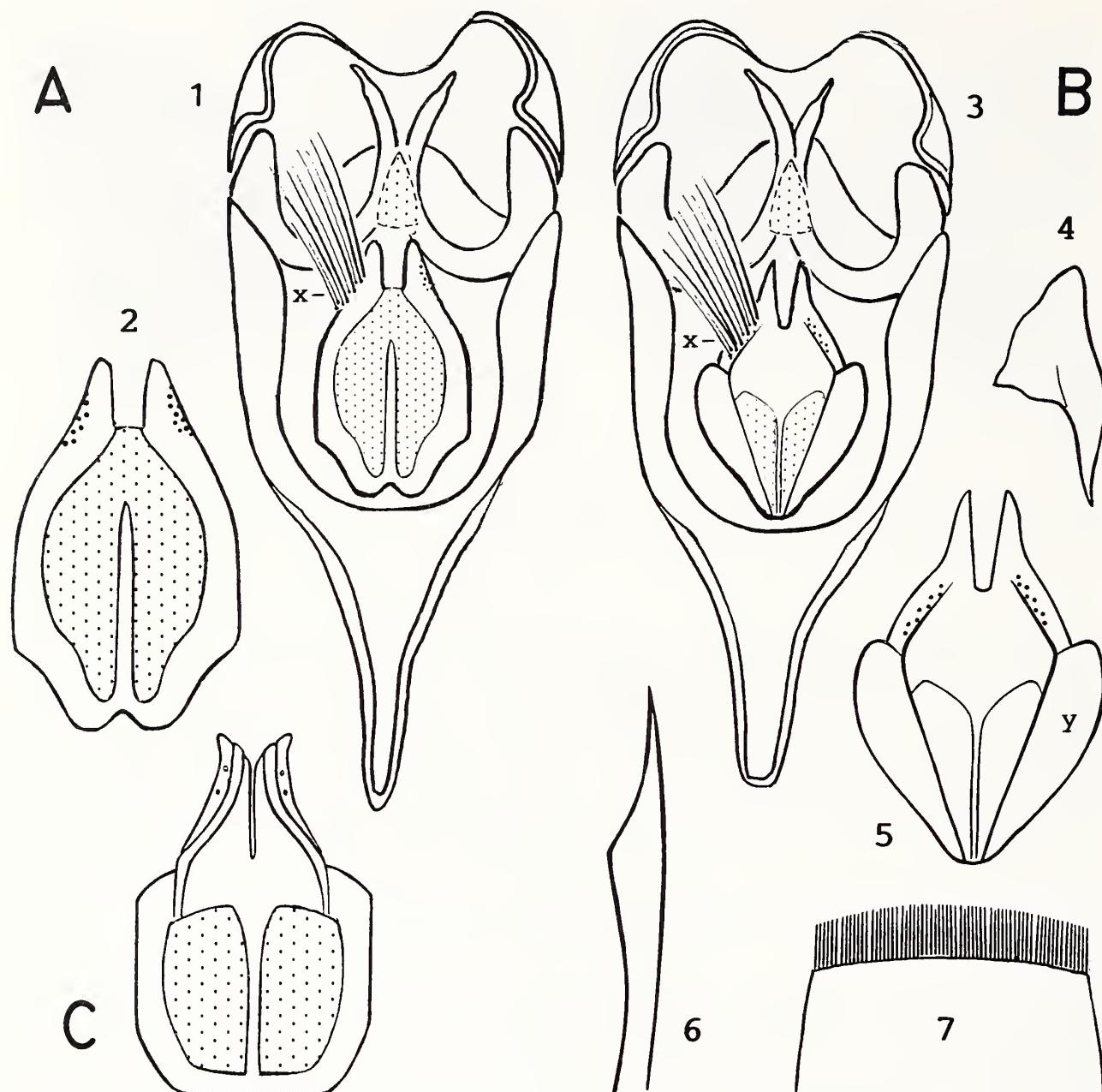


Fig. 2. Male genitalia of *Terra altilineata*, *T. cana* and *T. andevaga* (showing aspects illustrated and described in generic revision, Johnson, 1991a). A. *T. cana*, 1, genitalia (ventral view, x, terminal microtrichia); 2, valvae enlarged (ventral view). B. *T. altilineata*, 3, genitalia (ventral view, x, terminal microtrichia); 4, valvae, lateral view; 5, valvae enlarged (ventral view, y, distally shouldered element); 6, aedeagus terminus, lateral view; 7, terminal tergite, dorsal view. C. *T. andevaga*, valvae enlarged (ventral view). Stipples, areas of generally transparent sclerotization.

**Congeners and phylogenetic position.**—Regional congener *Terra cana* (Fig. 1B) is restricted to dense wet deciduous forest (700–1,250 m) in Tucumán and Jujuy provinces (Hayward, 1949, 1973; Johnson, 1991a). Contrasting *T. altilineata* on the hindwing under surface, *T. cana* has disjunct lunulate yellow-orange bands, an adjacent orange-bordered discal slash or line in cells RS and/or CuA1, and lunulate orange marginal spot in cell CuA1. Also, the forewing upper surface of *T. cana* exhibits wide blackish apices which obscure the usual distinction of the sexes by the males' dark forewing brand (Hayward, 1949, 1973; Johnson, 1991a, figs. 45, 47). The forewing brand in *T. altilineata* appears thinly elliptic and black against much

lighter brown wing apices, a condition typical of many other eumaeines (like taxa of species rich *Strymon* Hübner [Johnson et al., 1991]) but less like members of *Terra*, *Nesiostrymon* or their six immediate outgroup genera (Johnson, 1991b) with their mostly diffusive brands. Male genitalia in *T. cana* have brush organs attached along the vincular dorsum and, contrasting *T. altolineata*, exhibit an elongate saccus and terminally blunted aedeagus. Valvae of *T. cana* (Fig. 2A) are elliptic and of generally even contour, lacking any prominently shouldered elements. Valvae of *T. altolineata* only slightly resemble those of *T. andevaga* Johnson (TL submacrothermic rain forest, Pinchincha Dept., Ecuador, 1,325 m) which exhibit a robust, rather square, base contrasting short caudal extensions (Fig. 2C; Johnson, 1991a, fig. 74).

Considering cladograms of *Terra* and *Nesiostrymon* (Johnson, 1991b, fig. 1, 2, tables 1–4), the phylogenetic position of *T. altolineata* is obscured by the preponderance of female structural characters used in constructing the *Terra* ingroup cladogram. Geographic distributions of *Terra* species are greatly disjunct and interspecific differences in male genitalia (particularly valvae) do not reflect the intrageneric groupings suggested by wing stripe coloration and female genitalia. If, however, one assumes *T. altolineata* is part of the clade of *Terra* species restricted to South America (Johnson, 1991b, fig. 2, clade F), the following observations are consistent with character polarities recently attributed to the two genera.

For *T. altolineata*: (1) thin black under surface bands are a retained primitive character (consistent with the condition in *Nesiostrymon* and the reduced bands of the plesiomorphic Antillean endemic *Terra hispaniola* Johnson and Matusik); (2) widely shouldered valvae are most likely autapomorphic (non-homologous with distally lobate, ventrally multiplanar, conditions characterizing valvae of *Nesiostrymon* since, as typical of all *Terra* species, the valval ventrum in *T. altolineata* is of even contour [Fig. 2, B4]).

**Etymology.** The name combines the Latin roots for high (*altus*) and line (*linea*), referring to the high montane habitat and lineal under surface bands typifying the species.

#### ACKNOWLEDGMENTS

Robert C. and Barbara Eisele hosted the eleven member 1991 AMNH Argentine collecting expedition and chose Quebrada de las Cruces as one of the collecting sites. David and Kathy Matusik, Nick and Jake Pritzker, David and Karl Kroenlein, David and Seth Grae, and Steve Grossman also accompanied the author in the field. F. H. Rindge (AMNH) administered the AMNH Thecid Research Fund in support of this work.

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## OVIPOSITIONAL BEHAVIOR AND LARVAL DEVELOPMENT OF *APHIDENCYRTUS APHIDIVORUS* (HYMENOPTERA: ENCYRTIDAE), AN APHID HYPERPARASITOID

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**Abstract.**—In most hyperparasitoids, the female wasp attacks the primary parasitoid host either while the parasitized aphid is still alive or after the mummy is formed. *Aphidencyrtus aphidivorus* (Mayr) had been known to have a “dual” ovipositional behavior. Whether the adult female wasp attacked the primary parasitoid host through a live parasitized aphid or a mummified aphid, her egg was always deposited inside the host larva and not on the surface. The egg hatched inside the host larva, whereupon the hyperparasitoid larva first fed endophagously, and then ectophagously until the primary host larva was consumed. In “choice” experiments, 82% of the female *A. aphidivorus* wasps preferred to attack the primary parasitoid larva through the mummy, while only 18% chose the live parasitized aphids for oviposition.

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Aphid hyperparasitoids or secondary parasitoids can be divided into two categories based on their combined adult ovipositional and larval feeding behavior (Sullivan, 1986, 1987, 1988): (1) endophagous species in the families Charipidae (*Alloxysta*, *Phaenoglyphis*, *Lytoxysta*) and Eulophidae (*Tetrastichus*) in which the female wasp deposits her egg inside the primary parasitoid larva while it is still developing inside the live aphid (before the aphid is mummified); the egg does not hatch until the mummy is formed, at which time the hyperparasitic larva feeds internally on the primary parasitoid larval host, and (2) ectophagous species in the families Pteromalidae (*Asaphes*, *Pachyneuron*, *Coruna*) and Megasilidae (*Dendrocerus*). In these hyperparasitoids, the female wasp deposits her egg on the surface of the primary parasitoid larva after the aphid is killed and mummified. The hyperparasitic larva then feeds externally on the primary parasitoid larval host while both are still within the mummy.

Earlier studies on the biology of *Aphidencyrtus aphidivorus* (Mayr) (Encyrtidae) by Silvestri (1909), Griswold (1929), and Maple (1947) have documented “dual” ovipositional behavior in this species. Matteson (1977) reported that female *Aphidencyrtus aphidivorus* attack and oviposit into both live, parasitized aphids and mummified aphids. Details of this dual ovipositional behavior as well as the endo- and ectophagous development of the larva are described. In addition, the present laboratory study includes results of “choice” experiments by female *A. aphidivorus* between a primary parasitoid larval host in a live aphid or in a mummy, which might indicate preferential ovipositional behavior.

## MATERIALS AND METHODS

*Host plant and aphid.*—The broad bean, *Vicia faba* Linnaeus (Windsor variety), was used to rear the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), according to the method described by Bennett and Sullivan (1978). Plants and aphids were kept in a Percival bioclimatic chamber. The daytime regime had a photoperiod of 16 hr, a temperature of  $21.1 \pm 0.6^\circ\text{C}$  and  $75 \pm 5\%$  RH. At night the photoperiod was 8 hr of darkness, at  $15.5 \pm 0.6^\circ\text{C}$  and  $85 \pm 5\%$  RH. This bioclimatic chamber and the same environmental conditions were also used for separate, caged rearings of the primary parasitoids, hyperparasitoids, and for the "choice" experiments.

*Primary parasitoid and hyperparasitoid.*—*Aphidius smithi* Sharma and Subba Rao (Hymenoptera: Aphidiidae) was the primary parasitoid. Our colony originated from the Division of Biological Control Gill Tract (Albany), of the University of California at Berkeley. The secondary parasitoid or hyperparasitoid was *Aphidencyrtus aphidivorus* (Mayr) (Hymenoptera: Encyrtidae), which was reared from pea aphid mummies collected on alfalfa in Lafayette (Sussex County), New Jersey. In preparation for the photographic studies on egg deposition and larval development, we dissected a minimum of 30 live parasitized aphids and 30 mummified aphids.

"Choice" experiments.—After mating, 3 female *A. smithi* were introduced into a stinging-tube (glass cylinder 15 cm long and 3.3 cm in diameter and covered at both ends with a fine mesh organdy cloth, secured by rubber bands) containing a cut broad bean plant stem and 10–15 pea aphids always in the 4th instar. The stinging-tube was kept in the bioclimatic chamber for a 6 h ovipositional period. At the end of that time, the primary parasitoids were removed, and the aphids placed on growing bean sprouts and returned to the bioclimatic chamber. After 8 d, the aphid was killed by the primary parasitoid larva which had been feeding internally, and a mummy was formed, followed by pupation.

In the "choice" experiments, however, we started by first using one of the live, but parasitized, pea aphids that had been attacked by *A. smithi* 7 d earlier in a stinging-tube. At this stage of development, the parasitoid would be a 4th instar larva. This parasitized aphid was paired with a dead or mummified aphid (containing a 9-day old *A. smithi* prepupa or early pupa). Both were placed on a segment of broad bean leaf or stem in a Petri dish. One mated female *A. aphidivorus*, that had not been given the opportunity to oviposit previously, was put into the Petri dish equidistant between the two potential hosts (live parasitized aphid and mummy) and permitted to oviposit. The behavior of *A. aphidivorus* was observed continuously during a period of 2 hr maximum. Once the ovipositor was withdrawn from either one of the two potential hosts, the female *A. aphidivorus* was removed from the Petri dish. This might be much less than the 2 hr oviposition period, for in no case was the female permitted to oviposit into the 2nd host, nor remain beyond this maximum time limit even if she had not oviposited at all.

Once the hyperparasitoid was removed from the Petri dish, the mummy was placed in a gelatin capsule to await emergence of an adult wasp. The live aphid, however, was permitted to continue feeding on the broad bean for 48 hr or until it was killed and mummified by the *A. smithi* parasitoid larva inside. If a live aphid was not really parasitized and killed, then this particular paired replicate was discarded from the

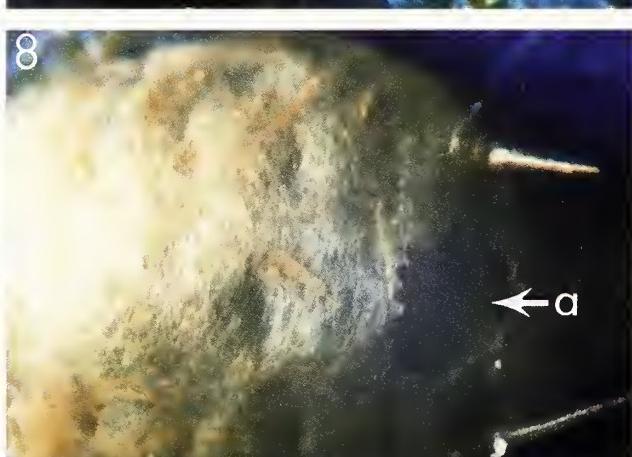
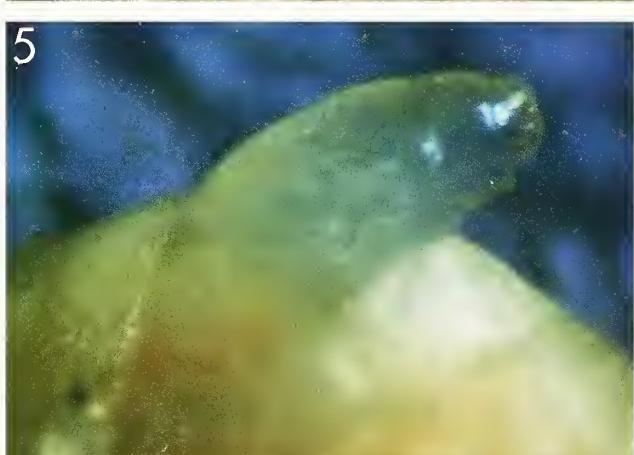
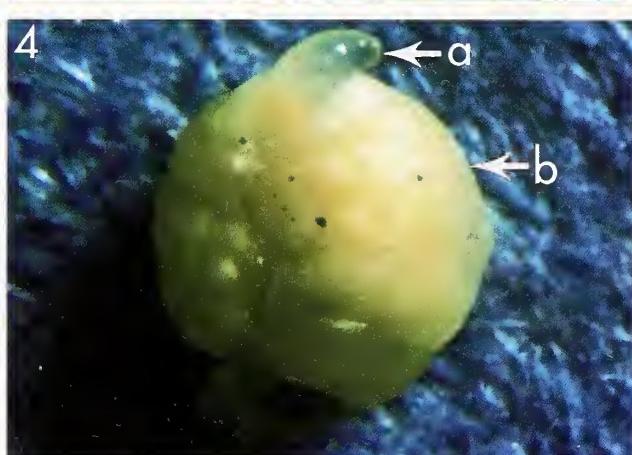
experiment. This newly formed mummy was also placed into a separate gelatin capsule. If the primary parasitoid, *A. smithi*, emerged (approximately 4 d after mummy formation), then oviposition by *A. aphidivorus* would not have occurred, or at least hyperparasitism would not have been successful. If on the other hand, the hyperparasitoid, *A. aphidivorus*, emerged (about 21–23 d after the attack), then this indicated effective hyperparasitism of whatever primary host was chosen: either in a live aphid or in a mummy. A total of 175 paired replicates was used in these choice experiments that resulted in 175 adult emergences of *A. aphidivorus*.

#### RESULTS AND DISCUSSION

*Oviposition into a live parasitized aphid.*—After initially antennating the live parasitized aphid (usually for less than a minute), the female *A. aphidivorus* mounted the dorsum, always facing caudally (Fig. 1). With her antennae pointed downward, motionless and touching the aphid, the female inserted her ovipositor through the integument of the aphid, pushing it into the hemocoel. With up and down thrusts, she probed for the larva of the primary parasitoid, and later dissections showed that the egg is laid internally in the *A. smithi* larva. After withdrawing her ovipositor, the *A. aphidivorus* sometimes host fed on the fluid that may ooze from the puncture hole of the aphid. The process of oviposition lasted 3–5 minutes.

*Oviposition into a mummy.*—This is similar to the behavior observed when attacking a live parasitized aphid. There was the usual antennating by the female, and she eventually climbed onto the dorsal surface of the mummified aphid. As in the behavior described when attacking a live parasitized aphid, the antennae were pointed downward and remained motionless, with the female facing caudally (Fig. 2). She then drilled a hole through the mummy wall with her ovipositor (Fig. 3), moving her body rapidly up and down. The ovipositor was pushed into the mummy, and as later dissections have shown, the egg was again laid inside the larva of *A. smithi*. This is unusual among hyperparasitoids that attack a primary parasitoid larva within a mummy, because the egg is normally deposited on the surface of the host in the mummy (Sullivan, 1986, 1987, 1988). After oviposition, the female withdraws her ovipositor and sometimes host feeds at the drill hole. However, a “feeding tube” is not formed as has been described for the host feeding behavior at the mummy by *Asaphes lucens* (Keller and Sullivan, 1976). The duration of oviposition into the mummy took 4–8 minutes, somewhat longer than when ovipositing into a live parasitized aphid. This was probably because of the need to penetrate the hard mummy wall.

*Developmental stages of Aphidencyrtus aphidivorus.*—As mentioned earlier, the female always placed the egg inside the primary parasitoid larva, never on the surface, regardless of whether the host was attacked in a live aphid or in an aphid mummy. When a 9-day old *A. smithi* was attacked through the mummy, this host was a prepupa or early pupa. In this case, *A. aphidivorus* required approximately 21 days to develop from egg deposition to adult emergence. However, if *A. smithi* was attacked while the aphid was still alive, the host was a 4th instar larva and the hatching of the egg was delayed 24–48 hr until the primary parasitoid larva killed the aphid and formed the mummy. This time difference was probably due to the developmental stage of the *A. smithi* host in relation to the aphid being alive or mummified, so that



the adult emergence of *A. aphidivorus* occurred 22–23 days after oviposition when a live parasitized aphid was attacked.

While still within the aphid mummy, the 1st and 2nd larval instars of *A. aphidivorus* fed endophagously within the primary parasitoid host, but the 3rd instar larva ate through the exoskeleton of the *A. smithi* larva and emerged from the host (Figs. 4–5). This occurs 9 d after egg deposition, and for the next 48 h, the *A. aphidivorus* larva continued to feed ectophagously until the primary parasitoid host was consumed.

When feeding ceased, the hyperparasitoid larva voided its meconium in the form of 35–40 small, sticky, yellow-orange, spherical pellets and became a prepupa (Fig. 6). These meconium pellets were easily distinguishable from the sausage-shaped, black meconium of *A. smithi*. After 48 hr, the pupa (Fig. 7) is recognizable and lasts 7–9 d, until the adult cuts its way out of the mummy by making an uneven, saw-edged exit hole (Fig. 8) in the aphid mummy, usually through the posterior dorsal surface. Then the adult *A. aphidivorus* pushed its head through the hole and pulled itself out of the mummy. This emergence occurs about 21–23 d after the original egg deposition; males usually emerged before females.

*Choice experiments.*—82% ( $N = 287$ ) of the *A. aphidivorus* females oviposited into mummies, while only 18% ( $N = 63$ ) chose the live parasitized aphids for oviposition.

When describing host selection by *A. aphidivorus*, Matteson (1977) reported that "Of the 60 hosts accepted for probing, 33 were mummies and 27 were live aphids. A total of 42 eggs were laid, 22 in *T. pallidus* larvae inside live aphids. These figures indicate no preference between hosts in live aphids and hosts in mummies for probing or oviposition." *Trioxys pallidus* (Haliday) is a primary parasite of the walnut aphid, *Chromaphis juglandicola* (Kaltenbach). Our data, on the other hand, are based on a different primary parasitoid and a different aphid species; and show a parametric statistically significant preference ( $P = <0.01$ ) by *A. aphidivorus* for hyperparasitism of the primary parasitoid larval host in mummies (82%) over that in live aphids (18%). Perhaps this preference is elicited by some factor or combination of factors, such as visual and/or chemical stimuli, but this important aspect is beyond the scope of the present study.

One might speculate about the evolution of this "dual" ovipositional behavior of *A. aphidivorus*. Data from related species are needed to clarify whether this hyperparasitoid primitively exhibited ovipositional behavior whereby it attacked the primary parasitoid larva in a live aphid, or whether it primitively waited for the host larva to kill the aphid, form a mummy, and only then oviposit into it. At present, it is not clear which of these two types of behavior is "primitive" or "advanced."



Figs. 1–8. 1. *Aphidencyrtus aphidivorus* ovipositing into live parasitized aphid ( $\times 10$ ); 2. *A. aphidivorus* ovipositing into mummified aphid ( $\times 6.4$ ); 3. *A. aphidivorus* with exserted ovipositor (a) drilling into mummified aphid ( $\times 13$ ); 4–5. Nine-day old 3rd instar *A. aphidivorus* larva (a) emerging from *Aphidius smithi* larva (b) and beginning to feed as an ectoparasitoid ( $\times 13$ ,  $\times 32$ ); 6. Ventral view of 11-day old *A. aphidivorus* prepupa (a) voiding meconium at caudal end (b) ( $\times 13$ ); 7. Ventral view of 16-day old *A. aphidivorus* pupa with meconium ( $\times 19$ ); 8. Saw-edged exit hole of (a) *A. aphidivorus* located on posterodorsal side of mummified aphid ( $\times 13$ ).

Also unusual about this hyperparasitoid is that unlike other genera of secondary parasitoids that attack the primary parasitoid through the mummy and deposit the egg externally on the surface of the host, *A. aphidivorus* oviposits inside the primary host within the mummy, thus behaving more like the endophagous hyperparasitoids that attack live parasitized aphids.

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## NOTES AND COMMENTS

*J. New York Entomol. Soc.* 100(3):533–534, 1992

### NEW DISTRIBUTIONAL RECORDS FOR SEMIAQUATIC HETEROPTERA, INCLUDING A *MICROVELIA* NEW TO THE UNITED STATES (HETEROPTERA: HYDROMETRIDAE, SALDIDAE, VELIIDAE)

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During a recent collecting trip to Arizona I collected a single female of *Microvelia rufescens* Champion along Bear Creek, about 6.5 miles west of the western edge of Coronado National Monument (Cochise Co., CL 2543, 2-IV-1991). This is a northwestern extension of the range of this species and the first record for the United States. The species occurs as far south as Guatemala and Costa Rica, and is widespread in central Mexico but rare in northern Mexico. The previous northernmost record was in northern Chihuahua (Smith, C. L. 1980, A taxonomic revision of the genus *Microvelia* Westwood [Heteroptera: Veliidae] of America including Mexico, unpublished dissertation, University of Georgia, Athens).

The following records extend the ranges of the listed species into states or provinces of North America not recorded in the recent catalog of North American Heteroptera (Henry, T. J. and R. C. Froeschner, Eds., 1988, Catalog of the Heteroptera, or True Bugs of Canada and the Continental United States, E. J. Brill, Leiden & New York). They are given so that they will be available before the next revision of that work. Collection abbreviations are given in the acknowledgments.

#### Hydrometridae

*Hydrometra martini* Kirkaldy. Colorado, Yuma Co., Hale Ponds, 6 mi NE of Hale, 10-VII-1987, J. T. Polhemus (JTPC).

#### Saldidae

*Micracanthia bergrothi* (Jakovlev). Quebec, R. Port-Daniel (Bona.), #17, 20-VIII-1975, L. LeSage (CNCI).

*Pentacora sphacelata* (Uhler). Quebec, Bécancour (Nicolet), #797, 16-VI-1979, L. LeSage (CNCI).

*Saldula opacula* (Zetterstedt). Ontario, Elmira, Salem Creek, #T4, 14-VIII-1977 and #T5, 7-VII-1977, L. LeSage (CNCI).

*Saldula orbiculata* (Uhler). Ontario, Elmira, Salem Creek, #T10, 20-VIII-1977, L. LeSage (CNCI).

*Teloleuca pellucens* (Fabricius). Quebec, Bécancour (Nicolet), #797, 16-VI-1979, L. LeSage (CNCI).

#### Veliidae

*Microvelia austrina* Torre Bueno. Kentucky, Fayette Co., Lexington, S. Travers (JTPC).

—*J. T. Polhemus, University of Colorado Museum, 3115 S. York, Englewood, Colorado 80110.*

*Acknowledgment.* For the opportunity to study a small collection of Saldidae that he collected, I am indebted to Laurent LeSage, Biosystematics Research Institute, Ottawa (CNCI). Material held in the Polhemus collection is coded (JTPC).

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## INSTRUCTIONS TO AUTHORS

The *Journal of the New York Entomological Society* publishes original research resulting from the study of insects and related taxa. Research that contributes information on taxonomy, classification, phylogeny, biogeography, behavior, natural history, or related fields will be considered for publication. The costs of publishing the Journal are paid by subscriptions, membership dues, page charges, and the proceeds from an endowment established with bequests from the late C. P. Alexander and Patricia Vaurie.

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**A FOSSIL *EMPICORIS* WOLFF  
(REDUVIIDAE: HETEROPTERA) FROM MEXICAN AMBER  
WITH REMARKS ON THE PHYLOGENETIC STATUS OF  
THE FOSSIL GENUS *ALUMEDA* POPOV**

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*Abstract.*—A fossil emesine reduviid (Heteroptera) is described from the Oligo-Miocene amber from the Simojovel formation of Chiapas, Mexico. The single specimen is described as a new species, *Empicoris electricus*. The characteristics of the fossil genus *Alumeda* are found to link the extant genera *Empicoris* and *Ctydinna*.

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Fossil Emesine reduviids are known from both European and New World deposits. A specimen assigned to the genus *Ploaria* Scopoli is reported from rock at Aix, France (Scudder, 1890). Bachofen-Echt (1949) illustrated an emesine nymph which was not assigned to genus, from the Baltic amber, and Schlee (1980) published a photograph of an emesine embedded in Dominican amber. Wygodzinsky (1966) mentions having seen a specimen of *Empicoris* Wolff in the Chiapas amber but offered no further elaboration. The most comprehensive reports on fossil emesines are those of Popov (1987a, b, 1989) who studied material from the Dominican amber. These included one species of *Malacopus* Stål, three species of an extinct genus *Alumeda* Popov, and a species of *Empicoris* in subfossil Dominican copal.

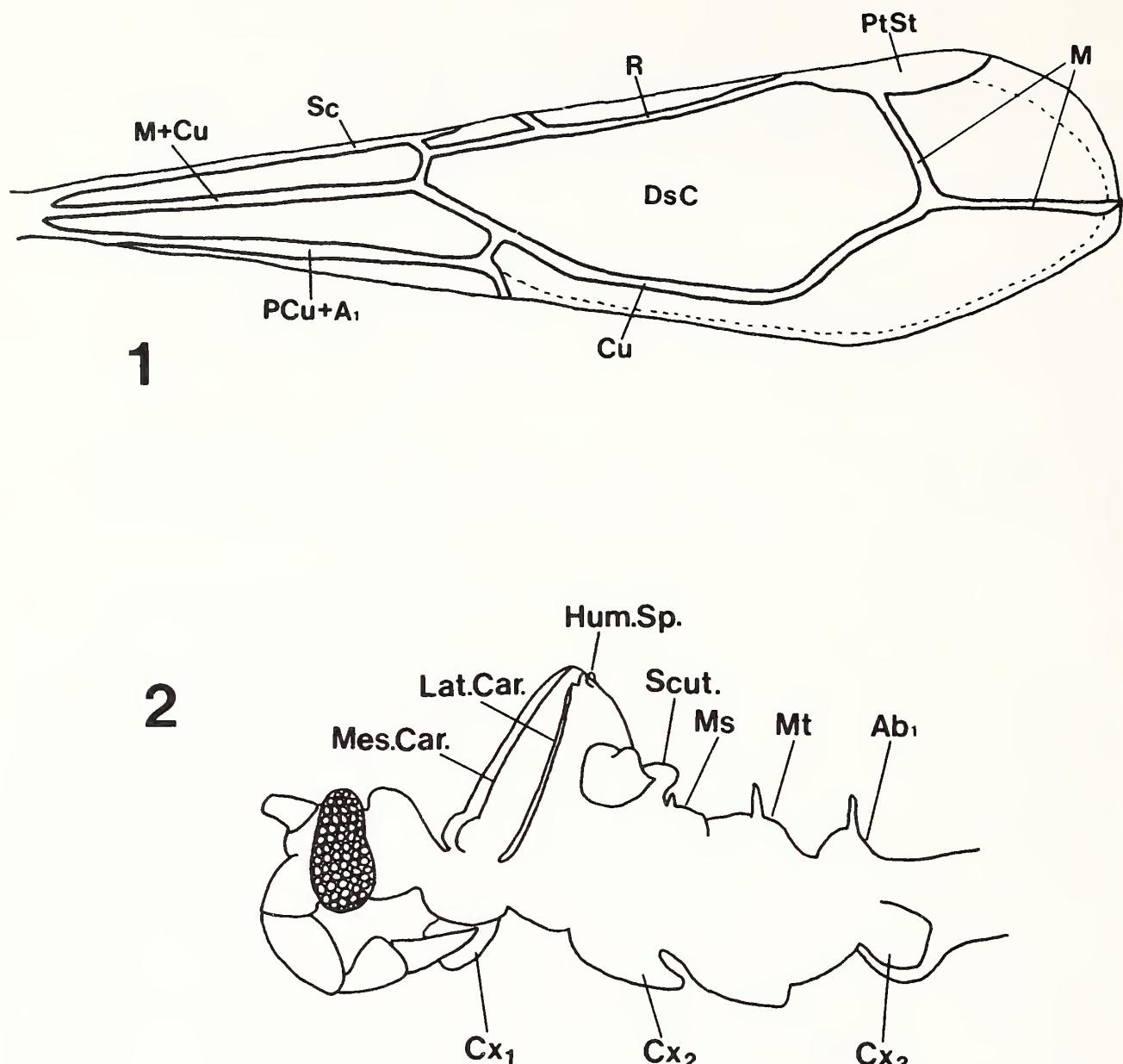
Wygodzinsky's (1966) report of *Empicoris* in Mexican amber is now confirmed, although his specimen was not available to me. The following description is based on a specimen purchased in Tuxtla Gutierrez, Chiapas, with a stated provenance of Simojovel, Chiapas, Mexico. The Simojovel formation, from which amber is mined, straddles the Oligo-Miocene boundary (Frost and Langenheim, 1974) giving an age of ca. 23 million years.

***Empicoris electricus*, new species**

*Description.* Narrow, elongate, small; length 3.8 mm. Thorax appearing unusually bilaterally compressed. Wings present, membranous with pattern of spots. Antennae and legs with numerous dark annuli; protarsi two-segmented.

Head constricted behind eyes; posterior lobe slightly larger than anterior lobe; eyes and antennal tubercle large. Rostrum without spines or stiff setae; segment II appearing distinctly swollen. Antennal segmental ratios I–IV: 0.09:1.00:0.40:0.15.

Pronotum with complete lateral carinae as well as pair of mesial carinae on anterior dorsum. Humerus with small, spinous tooth at dorsal terminus of each lateral carina. Posterior dorsal border of pronotum without medial tubercle or projection. Scutellum with non-spinous projection; mesonotum with small, median tubercle; metanotum and first abdominal segment each with prominent erect spine (Fig. 2).



Figs. 1–2. *Empicoris electricus*, n. sp. 1. Hemelytron with venation: M+Cu = Medial+Cubital vein, Sc = Subcostal vein, R = Radial vein, M = Medial vein, PCu+A<sub>1</sub> = Postcubital+Anal vein one, Cu = Cubital vein, DsC = Discal Cell. 2. Head and thorax, lateral view (legs, wings and antennae not shown): Mes. Car. = mesial carinae (=dorsal carinae or submedial carinae), Lat. Car. = lateral carinae, Hum. Sp. = humeral spine, Scut. = scutellum, Ms = mesonotum, Mt = metanotum, Ab<sub>1</sub> = first abdominal tergite, Cx = coxae. All figures drawn with Camera Lucida.

Hemelytron with pterostigma far from apex: distance from insertion of M vein on pterostigma to tip of pterostigma about half distance from latter to apex of wing. M+Cu vein fused to form single stem emitting from base of discal cell. Discal cell without smaller closed cell at its base; basal angle truncate; separated from costal margin by intervening membrane. R vein connected to margin of wing by two veinlets (sc-r crossveins). Cu vein bent in apical portion oblique to wing axis. False or spurious submarginal vein present along posterior and apical portion of wing (Fig. 1).

Profemur with posteroventral series of minute spinules, longer proximally; longest ca. one-third diam. of femur. Tarsomere II ca. twice length of I.

*Holotype.* Male. Mexico, Chiapas, Simojovel Area. Cat. No. DT-055. Embedded in a cut and polished piece of fossil amber, flat, tear-shaped, measuring 26 × 13 × 6 mm in dimension. Deposited American Museum Natural History, New York.

*Remarks.* *Empicoris* is a cosmopolitan genus of about 50 species of which five are reported to occur in Mexico (Maldonado-Capriles and Brailovsky, 1983). The fossil species *Empicoris electricus* is unique in having humeral spines, although *E. incredibilis* Wygodzinsky and *E. copal* Popov have flaps in the same position. Dorsal pronotal carinae (termed submedial carinae by Wygodzinsky [1966]) occur in *E. barberi* McAtee & Malloch and *E. mirabundus* Wygodzinsky. The carinae are more pronounced in the fossil species but this may be because the specimen is bilaterally compressed; possibly as a result of the heterogenous distortion common in amber fossilization. The thorax in *Empicoris* is typically dorso-ventrally compressed. The presence or absence of spines on the scutellum, mesonotum, metanotum and first abdominal tergite are important in species recognition. *Empicoris electricus* shares with *E. barberi* and *E. mirabundus* the absence of a scutellar spine commonly found in other species but has a metanotal spine that is absent in the latter two species. The new fossil species is also unusual in having the second rostral segment distinctly swollen. In the Emesinae the second rostral is at most slightly swollen (Wygodzinsky, 1966). A swollen second rostral segment is characteristic of the related subfamily Saicinae. However, in that subfamily the rostrum and venter of the head is bristled with spinous setae and the acetabulae of the procoxae are not directly forward (Blinn, 1990). In these regards the specimen is a typical emesine, and again the apparent condition may be an artifact of distortion in fossilization.

#### DISCUSSION

When Popov (1989) described the early Miocene fossil genus *Alumeda* he listed three characteristics by which it differed from all other ploarioline genera. These were (briefly): (1) the pterostigma shortened; (2) the base of the discal cell "shortly pointed"; and (3) the discal cell in broad contact with the wing margin. In fact these characters will not adequately separate *Alumeda* from all species of *Empicoris* including the fossil species described above. Popov reiterated these characters in a key to those emesine genera related to *Alumeda* and *Empicoris*, which have a single stem vein (M+Cu) emitting from the base of the discal cell. The key was modified from Wygodzinsky's (1966) key to genera of Ploariolini to include only the five extant genera with the single stem vein and the fossil genus *Alumeda*. The couplet [10(7)] leading to *Alumeda* and separating *Empicoris* and *Ctydinna* states: "Distance from apex of pterostigma to tip of forewing no less than twice as long as distance from pterostigmal apex to insertion of M on same; base of discal cell shortly pointed, only a basal quarter or fifth of anterior border of cell separated from wing margin and connected to it by one cross vein." Actually, in some common species of *Empicoris*, such as *E. vagabundus* (L.) and *E. orthoneuron* McAtee & Malloch, the ratio in the length of the distal pterostigma to the length to the wing tip, is twice as in *Alumeda*. Also, in the fossil species *E. electricus*, which has venation very similar to that of *E. vagabundus*, this ratio is 2×. With regard to the character of the discal cell relative to the wing margin; in most species of *Empicoris* the discal cell is separated from the wing margin by an intervening membrane and connected by two bridging cross-

veins. However, *E. orthoneuron* is like *Alumeda* spp. in having the discal cell in broad contact with the margin. Similarly, some Asian species, including the holarctic species *E. culiciformis*, have the discal cell in broad contact with the wing margin (Putshkov, 1989). Thus, most of the wing venation characters emphasized by Popov will not separate *Alumeda* from *Empicoris*. The only reliable venation character separating the genera is the presence of two sc-r crossveins in *Empicoris* and *Ctydinna* (only one in *Alumeda*). The presence of the proximal crossvein forms the angle which results in the discal cell base being truncate instead of pointed; Popov's second distinguishing characteristic for *Alumeda*.

Popov's (1989) and Wygodzinsky's (1966) key character separating *Empicoris* from *Ctydinna* will also separate *Alumeda*. *Empicoris* characteristically has lateral pronotal carinae that are lacking in *Alumeda* and *Ctydinna*. Bergroth (1909) proposed the separation of two genera *Ploiaroides* White and *Ploariola* Reuter (synonyms of *Empicoris*) based on the presence or absence of the pronotal carinae. McAtee and Malloch (1925) noted that the carinae varied from complete to reduced to obsolete (particularly in unnamed specimens from the South Pacific) and therefore disregarded the value of the character, stating that it was worth at most subgeneric distinction. Subsequently, China (1930) proposed the subgenus *Dictynna* for a species from Samoa in which a salient feature was the lack of lateral pronotal carinae. In his monograph, Wygodzinsky (1966) elevated *Dictynna* to full genus, changing the name to the anagram *Ctydinna* Wygodzinsky; *Dictynna* being preoccupied in the Hymenoptera. *Ctydinna* is monotypic; its one species *nitidicollis* China, has wing venation similar to that of a typical *Empicoris*. When China proposed *Dictynna* as a subgenus of *Empicoris* he emphasized the lack of an emargination on the posterior border of the basal abdominal sternite. Wygodzinsky (1966) characterized the posterior border of this sternite as "faintly emarginated," and did not include this character in the generic key. Thus, Wygodzinsky elevated the monotypic *Dictynna* to genus level while dispensing with the character considered by China to be its defining character, and emphasizing the character (lateral pronotal carinae) considered by McAtee and Malloch (1925) to be worth at most subgeneric distinction. In *Empicoris rubromaculatus* McAtee & Malloch, for example, the lateral carinae, though present, are greatly reduced.

Thus, *Ctydinna* and *Empicoris* are closely related and distinguished only by a character whose discreteness and significance is questionable. The fossil genus *Alumeda* differs from *Ctydinna* in wing venation as described by Popov (1989), and from *Empicoris* by the lack of lateral pronotal carinae. Whether these differences deserve generic or only subgeneric distinction is clearly subjective. A reanalysis of the character-states exhibited by the fossil genus *Alumeda* and the extant genera, *Empicoris* and *Ctydinna* indicates a closer relationship among them than prior treatments would suggest.

#### ACKNOWLEDGMENTS

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**DISCOVERY OF SEXUAL WING DIMORPHISM IN  
STAPHYLINIDAE (COLEOPTERA): “*OMALIUM*” *FLAVIDUM*,  
AND A DISCUSSION OF WING  
DIMORPHISM IN INSECTS**

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*Abstract.*—Wing reduction and wing dimorphism in both sexes of an insect species are widespread phenomena. Sexual dimorphism in wing development is less common, and is previously unrecorded in the large beetle family Staphylinidae. *Omalium flavidum* Hamilton, a little-known forest staphylinid widespread in northeastern North America, has unusual wing dimorphism: flightless females and males, with minute vestigial wings and modifications often associated with wing loss; and fully-winged males, with distinctly elongate antennae, elytra, and legs. Occurrence of this and other patterns of sex-linked wing dimorphism in insects is reviewed and discussed. *Omalium flavidum* is redescribed and illustrated and a lectotype is designated for the species.

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The presence of wings and the usually-associated ability to fly are conspicuous and fundamental features of most insects in the vast assemblage Pterygota. Nevertheless, secondary loss of wings in some descendants of winged insects has long been known (e.g., Wollaston, 1854, whose data were discussed by Darwin, 1859) and is quite widespread. In addition to orders whose members are universally wingless, strong wing reduction or loss has been recorded within all orders of insects except Odonata, Ephemeroptera, and Megaloptera (Roff, 1986a); although some Ephemeroptera have the hind wings vestigial or absent, they have not lost the ability to fly. Varying degrees of wing reduction have been recognized, which may be roughly categorized as: aptery, complete lack of wings; microptery, presence of very small wing vestiges (venation highly reduced or absent); and brachyptery, possession of distinctly shortened wings (venation almost normal to noticeably reduced, but apical region of wing strongly reduced). In fact, these are merely approximate points on a continuum of wing development, and additional terms have been proposed by some workers.

Most species are uniform with regard to wing development, but many show variation to different degrees. The occurrence of some kind of wing dimorphism (or polymorphism) within species is reasonably common in many orders of insects (Roff, 1986a and references therein; CSIRO, 1970). There are, however, different classes of dimorphism with respect to the distribution of morphs within the sexes, and some of these classes appear to be far more common than others (see Discussion and Table 4). The type of wing dimorphism reported here in *Omalium flavidum* Hamilton, namely micropterous females and both micropterous and macropterous males, appears to be extremely rare, as it has seldom been reported.

**MATERIALS, METHODS, AND TERMINOLOGY**

I examined a total of 161 specimens of *Omalium flavidum*, originating from or deposited in the following collections (acronyms as used in collection records, Appendix B):

AMNH	American Museum of Natural History, New York
ANMT	A. F. Newton, Jr. and M. K. Thayer collection, Chicago
CAS	California Academy of Sciences, San Francisco
CM	Carnegie Museum of Natural History, Pittsburgh
CNC	Canadian National Collection, Ottawa
CU	Cornell University, Ithaca, New York
FMNH	Field Museum of Natural History, Chicago
GHN	G. H. Nelson collection, Pomona, California
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
UNH	University of New Hampshire, Durham, New Hampshire
USNM	National Museum of Natural History (Smithsonian Institution), Washington

Specimens were examined dry (point- or card-mounted), in alcohol, and KOH-cleared and slide-mounted. Drawings were made with a drawing tube on a Leitz Dialux 20 differential-interference contrast microscope; photomicrographs were taken on the Dialux with a Leitz Vario Orthomat 2 apparatus. Scanning electron microscopy was done with an AMRAY 1810; the specimens used were cleaned, critical-point dried, and gold-coated. Measurements, made with an ocular micrometer in a Leitz stereomicroscope, are defined as follows (all viewed perpendicular to line of measurement):

- Antennal length: from constriction at base of scape to apex of last antennomere
- Head length: along midline, clypeal apex to posterior ocellar margins, dorsal view
- Head width: maximum width including eyes, dorsal view
- Ocular length: maximum longitudinal distance, dorsal view
- Interocular width: minimum distance between dorsal margins of eyes, dorsal view
- Pronotal length: along midline, base to apex, dorsal view
- Pronotal width: maximum width, dorsal view
- Elytral length: longitudinal from front of humerus to elytral apex, dorsal view
- Elytral width: maximum combined width of closed elytra, dorsal view
- Hind tibial length: base to apex, not including apical spurs or setae
- Hind tarsus, tarsomeres 1–4: base of tarsomere 1 to base of tarsomere 5
- Hind tarsus, tarsomere 5: base to apex, not including claws
- Metathoracic length: along midline, apex of mesosternal intercoxal process to apex of metasternum, ventral view
- Metathoracic width: maximum width (at posterior margin), ventral view

Calculated figures in Tables 1 and 2 are:

$$\begin{aligned}\text{Calculated length} &= \text{Head length} + \text{Pronotal length} + \text{Elytral length} \\ \text{Eyes, } 2 \times \text{width} &= \text{Head width} - \text{Interocular width} \\ \text{Dorsal "area" (both eyes)} &= (\text{Head width} - \text{Interocular width}) \times \text{Ocular length}\end{aligned}$$

Statistical analyses (*t*-tests for pairwise differences between means,  $F_{\max}$  tests for homogeneity of variances) were done using the computer program MYSTAT, a product of SYSTAT, Inc. Because of the disproportionately high number of winged males in the material available, some problems with condition of specimens, and receipt of some material very late in the project, not all specimens were measured. The map was produced using QUIKMap (ver. 2.5), a product of Axys Systems, Inc.

I did not attempt an exhaustive literature search regarding wing reduction or dimorphism/polymorphism in insects. Literature on Coleoptera was searched more thoroughly than that on other orders, and the paper is mainly focused on Coleoptera. In the Discussion, ordinal placement of non-Coleopteran families is indicated.

Some species include individuals with only slight reduction in wing length, which are probably capable of flight; these individuals are here lumped with fully-winged individuals as macropterous (=fully-winged), since they are functionally so. For simplicity, forms incapable of flight are likewise generally lumped together. For brevity, I will often refer to brachypterous or micropterous forms as -W and macropterous forms as +W. Likewise, for simplicity of expression, I will use the term wing dimorphism to encompass both dimorphism and polymorphism of wing development, since aptery, microptery, and brachyptery are functionally the same with respect to flight capability.

#### *OMALIUM FLAVIDUM*

*Omalium flavidum* Hamilton is a widespread (Fig. 1) but very poorly known eastern North American species of staphylinid beetle. It belongs to the mainly temperate subfamily Omaliinae, and more specifically to the tribe Omaliini. Its placement in Omaliini is supported by three derived characters (Thayer, in preparation): the presence of a (vestigial) seta-edged groove (Fig. 22) on the third abdominal tergite (Hammond, 1979, figs. 16, 17), a two-chambered sclerotized spermatheca in the female (Fig. 30), and the extremely reduced anterior tentorial arms. Females and micropterous males also have tarsi characteristic of Omaliini, with the basal four tarsomeres together shorter than the fifth (Hatch, 1957; Moore and Legner, 1979).

When Hamilton (1896:347) described *Omalium flavidum*, the genus *Omalium* was generally used in a much broader sense than now. There is no basis for placing the species in *Omalium* as now recognized (e.g., Lohse, 1964; Moore and Legner, 1979; Zanetti, 1987), since *O. flavidum* lacks the characteristic carinate mesosternum and aedeagal structure of that genus (abparameral surface of median lobe truncate well before apex; see Zanetti, 1987, figs. 45, 46, 47a–p). The head structure of *O. flavidum* is suggestive of the Palearctic genera *Carcinocephalus* and *Dialycera*, but I prefer not to change its generic placement or erect a new genus before completing a comprehensive study of the genera of Omaliini (Thayer, in preparation). Since the species was originally so incompletely described, I provide a more thorough redescription in Appendix A of the present paper.

*Sexual and male dimorphism.* Since this species was named and described very briefly almost 100 years ago (Hamilton, 1896), its only mention in the literature has been in catalogs. I have discovered that *O. flavidum* is a dramatically variable species, consisting of macropterous males (Figs. 4, 16a) and extremely micropterous females and males (Figs. 5, 16b). According to the conventions given above, *O. flavidum* (or

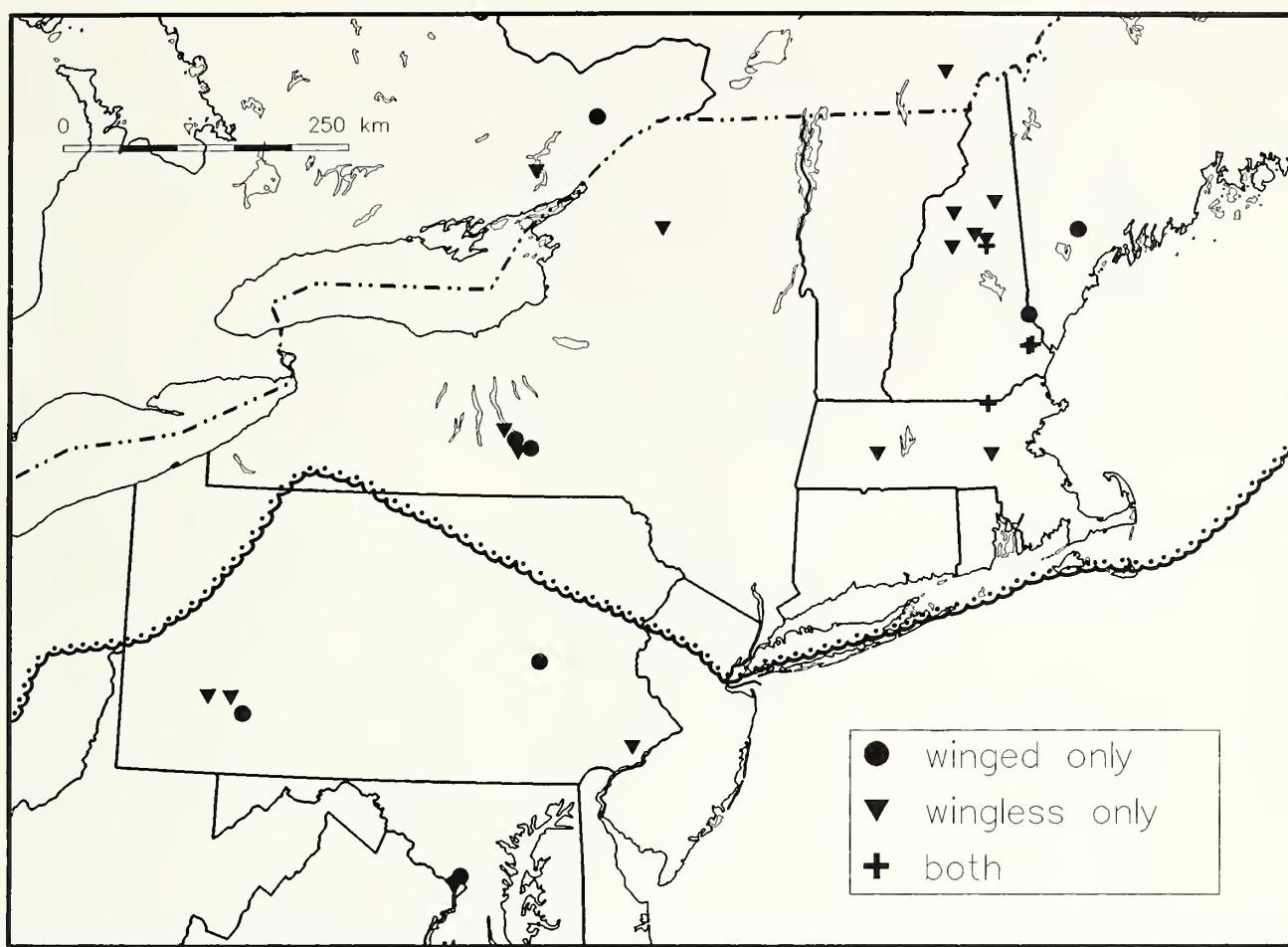
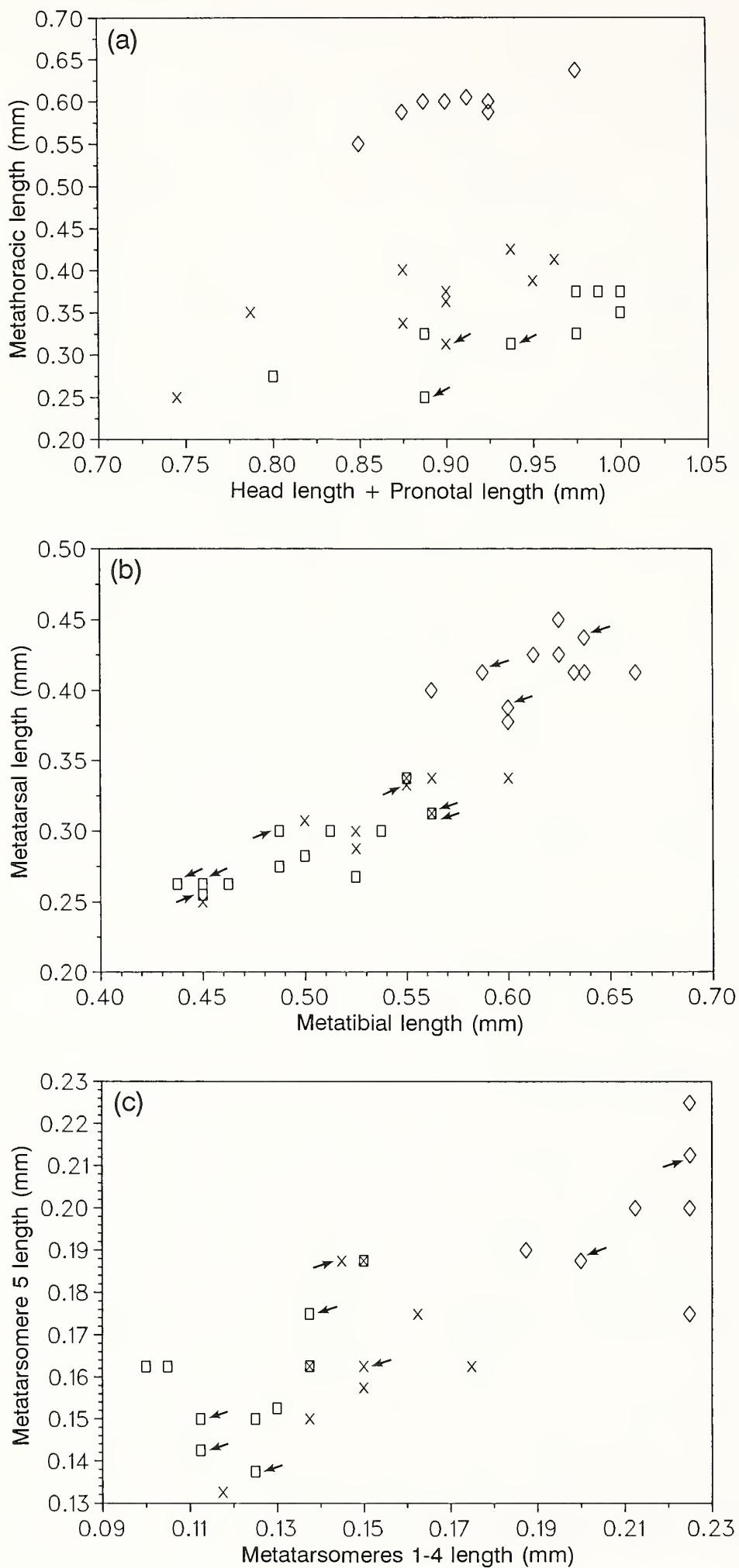


Fig. 1. Northeastern U.S.A. and adjacent Canada, showing known distribution of *Omalium flavidum* Hamilton. Scalloped and dotted line shows approximate maximum limit of late Wisconsinan glaciation (after Morgan and Morgan, 1981).

the males collectively) can thus be called  $\pm$ W. Micropterous ( $-W$ ) individuals, including the syntype specimens, are all similar in appearance and readily distinguishable from the  $+W$  males (compare Figs. 4, 6, 8, 16a, 17, 23, with 5, 7, 9, 16b, 18, 24). Table 1 summarizes a number of features differentiating the morphs and Table 2 quantifies these and some other mensural characters.

Both wing morphs of *O. flavidum* differ from macropterous species of Omaliini in readily observable ways. The  $-W$  forms ( $\delta$  and  $\varphi$ ) have several modifications (derived features) often associated with wing loss: shortened elytra (common in  $-W$  Staphylinidae); reduced eyes, elytral humeri, and metathorax (Fig. 2a); strengthened elytral interlocking; loss of abdominal tergal wing-folding patches; and ( $\varphi$  only) loss of the palisade fringe on tergite 7. The  $+W\delta$  differ from other macropterous Omaliini (and  $-W$  *O. flavidum*) in having: (1) filiform (instead of clavate) antennae, composed of slightly elongate antennomeres (Fig. 4); (2) elongate tarsi and tarsomeres (Figs. 2b, c, 17); and (3) very long elytra (Fig. 4). The first two of these resemble probably-primitive features for the subfamily, but appear to be secondarily derived within Omaliini; the third occurs sporadically within Omaliinae (presumably having evolved several times), but is unknown to me among other Omaliini.

*Conspecificity of morphs.* Despite these dramatic differences between  $+W$  and  $-W$  morphs, there are several morphological characters that argue for the different wing



morphs being very closely related, and indeed conspecific. A feature unique to *O. flavidum* is the form of the empodial setae. Normally, Omaliinae (like most Staphylinidae) have a pair of subequal setae on each tarsal empodium. In some taxa one of the pair is lost, leaving the empodium unisetose (e.g., in the genus *Empelus*, related to Omaliinae, Thayer, 1987; Newton and Thayer, 1992); in others, for instance Corneolabiini (see Thayer, 1985), both are lost and the empodium is asetose. All morphs of *Omalium flavidum*, however, have one empodial seta greatly reduced in size and the other distinctly longer than usual (Fig. 19). I interpret this modification as a unique autapomorphy linking the morphs, although not necessarily indicating conspecificity. (*Carcinocephalus (Scribaia) blandus* (Luzé) has unequal empodial setae, but the shorter one is much less reduced and the difference between the two is less.)

Male genitalia of Omaliinae, including Omaliini, usually provide characters diagnostic at the species level (Steel, 1957, 1960, 1964; Lohse, 1964; Smetana, 1981, 1985; Thayer, 1985; Zanetti, 1987; Watanabe, 1990), as in most Staphylinidae (and indeed most Coleoptera and many other Insecta). In several genera of Omaliini, there are also male secondary sexual characters of the abdominal sternites, hind tibiae, and/or hind coxae that differ between and serve to distinguish species (e.g., Steel, 1957; Zanetti, 1987; Watanabe, 1990; Thayer, in preparation). The aedeagi of the male morphs of *O. flavidum* (Fig. 28) are indistinguishable from each other in size, external morphology, and armature of the internal sac. In addition, the arrangement of setae at the apices of abdominal sternites 7 and 8 (Fig. 25) and the sclerotization pattern at the apex of sternite 8 (Fig. 25) are the same in both morphs and different from any I have seen in other Omaliinae. In addition, males of *O. flavidum* have dense long blunt sensilla on antennomeres 3–11; it is very unusual, if not unique among at least Omaliini, to have these sensilla located more basally than antennomere 6.

The pronotum of *O. flavidum* (females and both male morphs; Figs. 4, 5) is distinctive in having a raised median triangular area containing an impression on either side of the raised midline. This is unlike the pronotum of any other Omaliini known to me.

At least some genera of Omaliini show interspecific variation in the structure of the defensive gland associated with the anterior projection on abdominal sternite 8. These structures appear to be identical in females and the two male morphs of *O. flavidum* (Fig. 26). Similarly, the occurrence of apical membranous fringes (and their form, if present) and the distribution of apical spinules and ventral sensory structures (sensilla basiconica?) on the epipharynx varies among genera and, to some extent, species of Omaliinae. Females and both male morphs of *O. flavidum* all have the same epipharyngeal ornamentation (Fig. 14), which is distinguishable (albeit some-



Fig. 2. *Omalium flavidum* Hamilton. (a) Metathoracic length vs. Head length + Pronotal length; (b) Metatarsal length vs. Metatibial length; (c) Length of metatarsomere 5 vs. combined length of metatarsomeres 1–4. ◇ +W♂, × -W♂, □ ♀. Arrows mark points representing specimens whose measurements are not included in Tables 1 and 2 because all their measurements could not be taken.

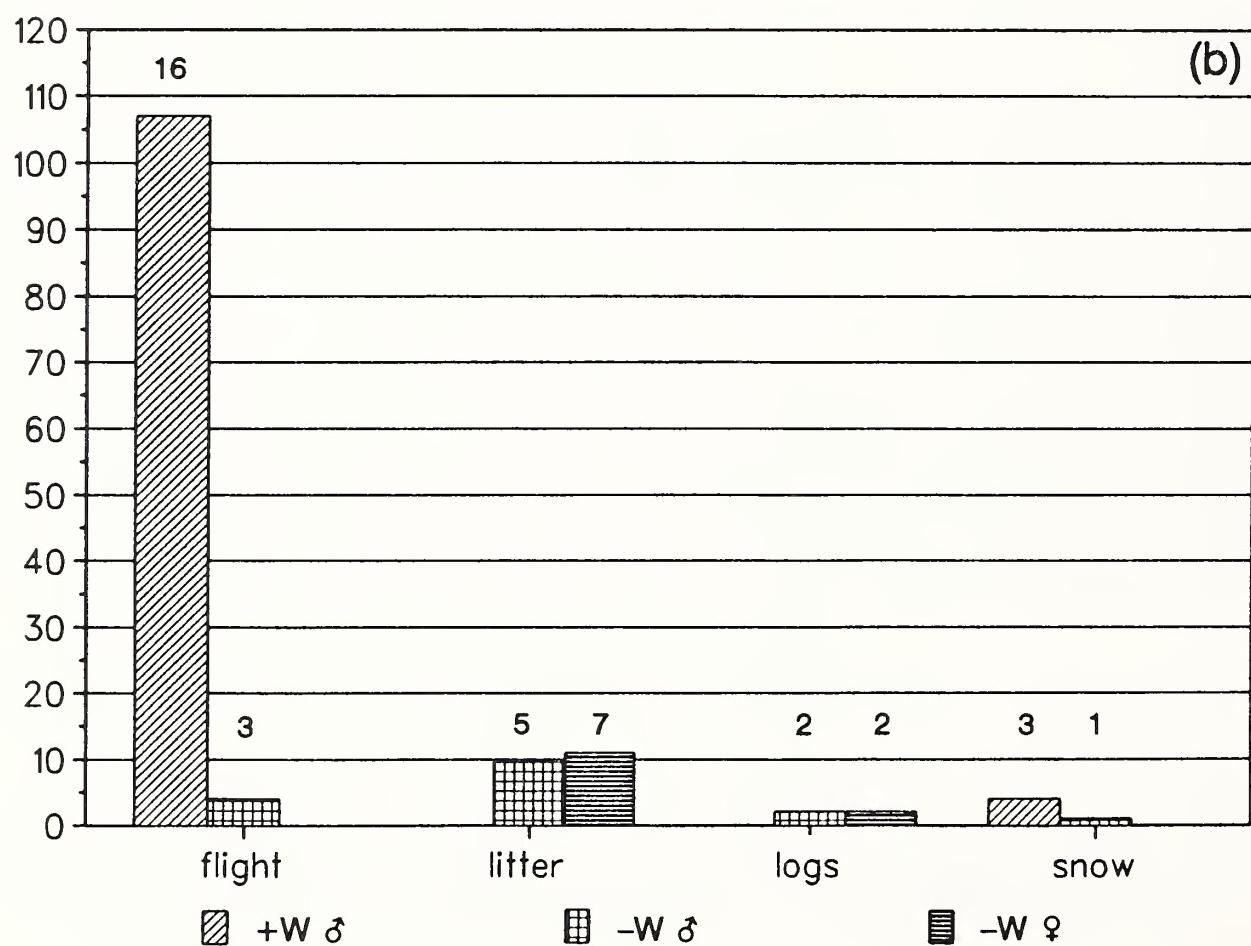
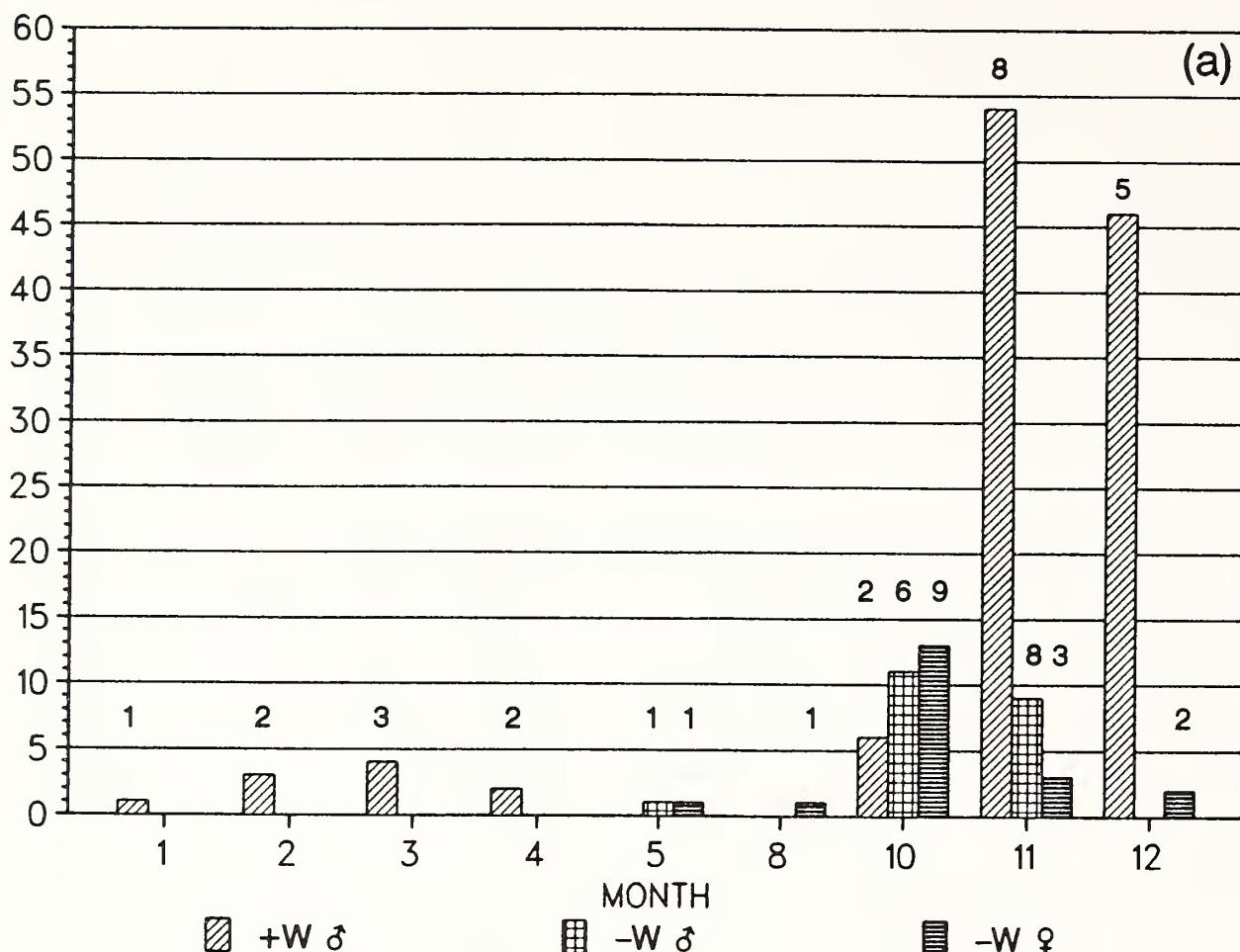


Table 1. Differences among wing morphs of *Omalium flavidum* (qualitative characters and means of some quantitative characters and ratios). See Table 2 for sample sizes, additional mensural characters, and standard deviations of measurements. All measurements are in mm.

Feature	$\delta +W$	$\delta -W$	$\varphi (-W)$
Color	Dark brown (almost black) to reddish-brown	Reddish-brown; elytra lighter, abdomen darker	Head reddish-brown, rest yellowish- to reddish-brown
Antennae	Long (1.56)	Short (1.18)	Short (1.07)
Antennomeres	Elongate (Fig. 4)	Shorter (Fig. 5)	Shorter ( <i>cf.</i> Fig. 5)
Eye size	Larger (Fig. 4)	Smaller (Fig. 5)	Smaller ( <i>cf.</i> Fig. 5)
•Ocular length	0.17	0.12	0.12
•2 x Width	0.15	0.11	0.10
•Dorsal "area"	0.03mm <sup>2</sup>	0.01mm <sup>2</sup>	0.01mm <sup>2</sup>
Elytral length	1.47	0.78	0.80
Elytral humeri	Normal, prominent (Fig. 4)	Reduced (Fig. 5)	Reduced ( <i>cf.</i> Fig. 5)
Elytral locking	Loose	Tightly interlocked with each other and scutellum (not fused)	Tightly interlocked with each other and scutellum (not fused)
Wings	Fully developed, ca. 4mm long (Fig. 16a)	Small stubs < 0.1mm long (Fig. 16b)	Small stubs < 0.1mm long (Fig. 16b)
Metathoracic length	Longer (Fig. 2a), 0.60	Shorter (Fig. 2a), 0.37	Shorter (Fig. 2a), 0.35
Hind tarsi	Longer (0.42), tarsomere 5 relatively short (Figs. 17, 2b-c)	Shorter (0.31), tarsomere 5 relatively long (Figs. 18, 2b-c)	Shorter (0.29), tarsomere 5 relatively long (Figs. 2b-c)
•Tarsal length/ Hind tibial length	0.67	0.58	0.56
•Tarsomere 5 length/ Tarsomeres 1-4 together	0.92	1.07	1.29
Basal abdominal spiracles (1-3)	Larger (Figs. 4, 6, 21)	Smaller (Figs. 5, 7, 22)	Larger ( <i>cf.</i> Figs. 4, 6, 21)
•Spiracles 1-3 compared to 4	Distinctly larger	Slightly larger	Distinctly larger
Abdominal wing- folding patches	Present on tergites 4 and 5 (Fig. 23)	Absent (Fig. 24)	Absent
Tergite 7 palisade fringe	Present (Fig. 10)	Present (Figs. 11-12)	Absent

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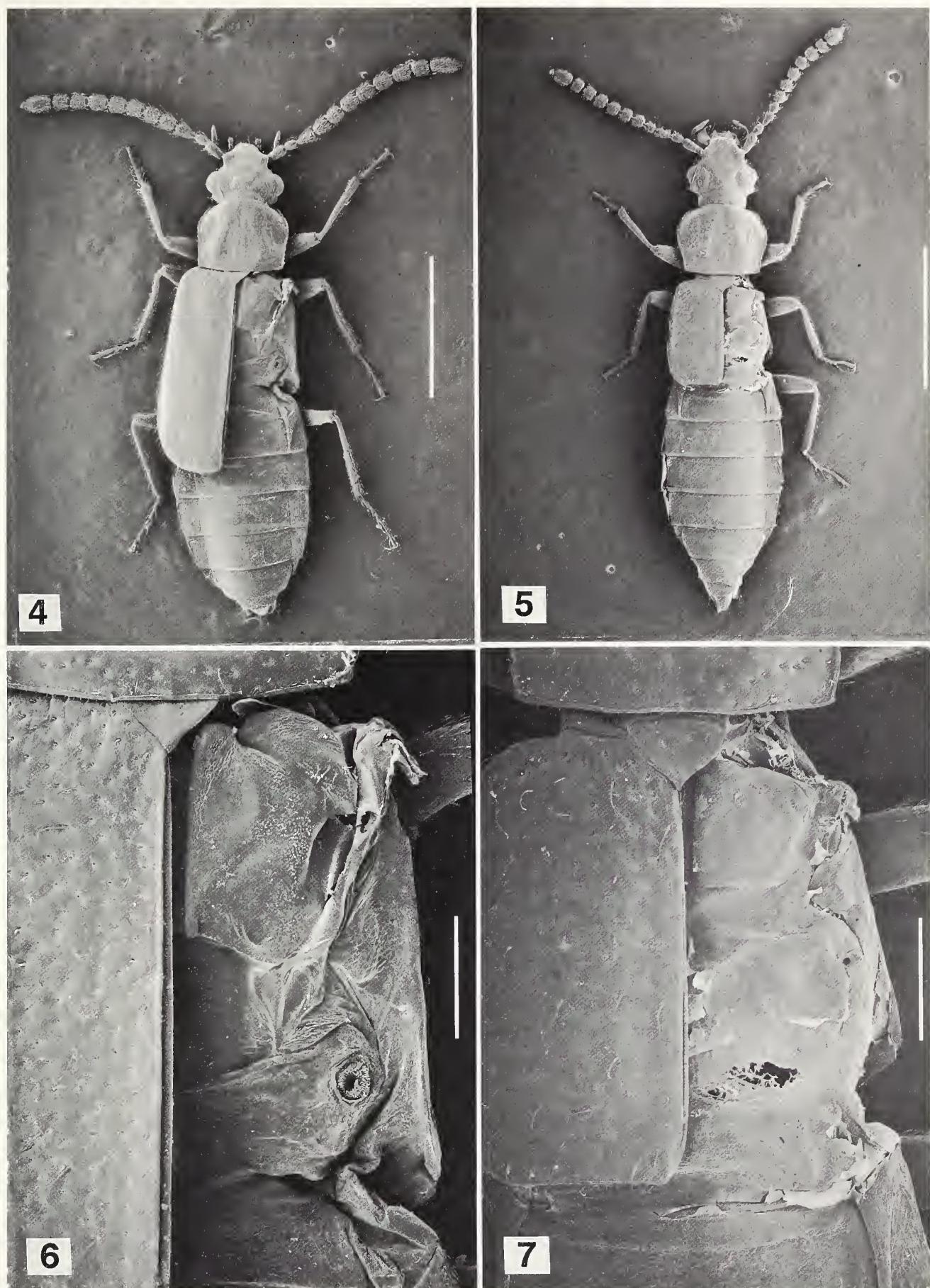
Fig. 3. *Omalium flavidum* Hamilton. (a) Number of specimens of each morph seen, by month, with number above each bar indicating number of samples included; one collection of 2-W ♀ in February not included; (b) Number of specimens of each morph seen, by generalized microhabitat, with number above each bar indicating number of samples included; "flight" includes intercept traps and "in flight."

Table 2. Mensural characters of wing morphs of *Omalium flavidum*. Mean  $\pm$  standard deviation for indicated sample size (N) of each morph. Boldfaced entry indicates mean of that feature for that morph is significantly different (by t-test) from means of both other morphs at the  $P \leq 0.001$  level or at the higher (still  $P \leq 0.05$ ) probability level indicated. All features with means differing significantly between morphs had variances not differing significantly ( $P \leq 0.05$ ) among morphs, so the t-test is appropriate. Non-bold means with no P given are not significantly different from unmarked means of the other morphs at the  $P \leq 0.05$  level. Means of ratios are the means of individual ratios, not ratios of mean measurements. All measurements in mm.

Measurement or ratio	$\delta +W$	$\delta -W$	$\varphi (-W)$
(N)	8	9	7
Calculated length	<b><math>2.38 \pm 0.09</math></b>	$1.66 \pm 0.15$	$1.74 \pm 0.14$
Antennal length	<b><math>1.56 \pm 0.10</math></b>	<b><math>1.18 \pm 0.11</math></b> ( $P \leq 0.045$ vs. $\varphi$ )	<b><math>1.07 \pm 0.08</math></b>
Head length	$0.41 \pm 0.02$	$0.39 \pm 0.03$	$0.42 \pm 0.04$
Head width	$0.53 \pm 0.02$	$0.50 \pm 0.04$	$0.54 \pm 0.05$
Ocular length	<b><math>0.17 \pm 0.07</math></b>	$0.12 \pm 0.01$	$0.12 \pm 0.01$
Interocular width	$0.38 \pm 0.02$	$0.39 \pm 0.04$	<b><math>0.44 \pm 0.03</math></b> ( $P \leq 0.002$ vs. $+W\delta$ ) ( $P \leq 0.011$ vs. $-W\delta$ )
Pronotal length	$0.50 \pm 0.02$	$0.50 \pm 0.05$	$0.53 \pm 0.04$
Pronotal width	$0.61 \pm 0.02$ ( $P \leq 0.019$ vs. $\varphi$ )	$0.62 \pm 0.06$	$0.67 \pm 0.05$
Elytral length	<b><math>1.47 \pm 0.06</math></b>	$0.78 \pm 0.09$	$0.80 \pm 0.07$
Elytral width	<b><math>0.97 \pm 0.05</math></b>	$0.77 \pm 0.08$	$0.83 \pm 0.07$
Hind tibial length	<b><math>0.62 \pm 0.03</math></b>	$0.54 \pm 0.04$	$0.51 \pm 0.03$
Hind tarsus, length tarsomeres 1-4 combined	<b><math>0.22 \pm 0.02</math></b>	<b><math>0.15 \pm 0.02</math></b> ( $P \leq 0.003$ vs. $\varphi$ )	<b><math>0.13 \pm 0.02</math></b>
Hind tarsus, length tarsomere 5	<b><math>0.20 \pm 0.02</math></b>	$0.16 \pm 0.02$	$0.16 \pm 0.01$
Metathoracic length	<b><math>0.60 \pm 0.02</math></b>	$0.37 \pm 0.05$	$0.35 \pm 0.04$
Metathoracic width	<b><math>0.83 \pm 0.05</math></b> ( $P \leq 0.002$ vs. $\varphi$ )	$0.65 \pm 0.05$	$0.70 \pm 0.07$

times subtly) from that of numerous other Omaliinae examined (Thayer, unpublished). Thus, characters on several parts of the body support the idea that the three forms discussed belong to a single dimorphic species.

*Distribution and ecology.* No additional collection records have been published since *O. flavidum* was described; the species is, in fact, distributed far more widely than just western Pennsylvania (type-locality "near St. Vincent"). As shown in Figure 1, *O. flavidum* occurs in the northeastern U.S. (District of Columbia and western Pennsylvania to Maine) and southeastern Canada (extreme southeastern Ontario and southern Québec). Relatively little habitat information is available for most collec-



Figs. 4–7. *Omalium flavidum* Hamilton. 4. Habitus, dorsal view, right elytron and wing removed, +Wδ. 5. Same, -Wδ. 6. Detail of pterothorax, dorsal view, +Wδ. 7. Same, -Wδ. (Scale line: Figs. 4–5, 1 mm; Figs. 6–7, 200 μm.)

tions of *O. flavidum* (Appendix B), but it appears to be a forest-associated species. From explicit ecological data associated with some specimens and inference from locality and potential-vegetation data (Küchler, 1964) for others, it appears that *O. flavidum* occurs in Appalachian oak, northern hardwood, and northern hardwood-spruce-fir forests (classification according to Küchler, 1964). Its distribution in a densely (human-) populated and heavily-collected area makes it surprising that *O. flavidum* has been so seldom collected. The reason, as with some other Omaliinae (e.g., *Glypholoma rotundulum*, Thayer and Newton, 1979; *Omalorphanus aenigma*, Campbell and Chandler, 1987), appears to be its seasonality, presumably reflecting a preference for (or at least tolerance of) cool temperatures. Available records are concentrated in October through December, with activity (as indicated by trap catches) continuing through the winter (Fig. 3a). Only five collections of one individual each have been made from April through September (Fig. 3a), the more usual entomological collecting season in the area.

Of the 163 specimens examined (116 +W males, 23 -W males, 24 -W females), some ecological or microhabitat data are available for 141; these are plotted in generalized terms in Figure 3b. The relatively large number of +W males in flight intercept traps (mostly from four samples at three different sites; see Appendix B) indicates that they do fly, although the presence of two -W males in one sample and one each in two others suggests that the traps also acted as pitfall traps to a limited extent (see Chandler, 1987). Forest leaf and log litter are the only microhabitats from which *O. flavidum* has been collected, but the relatively low number of individuals thus collected (compared to flight intercept traps) and the absence of +W males in those collections raise the question of whether that is their real microhabitat. More investigation of the litter fauna in late autumn and winter could show them to be more abundant there than is now apparent; the species may occupy a more specialized microhabitat, such as mammal or bird nests. The few specimens cleared had no visible gut contents; the beetles are probably extra-orally digesting predators.

The available data show no obvious geographical pattern in the distribution of +W and -W males of *O. flavidum*. Both forms occur more or less throughout the species' range (Fig. 1) and both forms have been collected at four sites and three additional pairs of close sites. Eight sites are represented in collections by only +W males, 5 by only -W males, 7 by only females, 4 by only -W males and females, 2 by only males (+W and -W), and 2 by all forms.

*Are there really no winged females?* One must consider whether present collections accurately reflect the nature of the species or the lack of winged females is an artifact of relatively small sample size. A reasonable starting point in assessing this question is the null hypothesis that winged females of *O. flavidum* actually exist at the same within-sex frequency as winged males. (This is the case for, e.g., the omaliine *Glypholoma rotundulum*; see Discussion.) Testing this null hypothesis using all available data (listed in Appendix B) results in decisive rejection at the  $P = 0.05$  level (Table 3,  $\chi^2$  and  $P$  columns, line 1). The large number of winged males from four flight intercept trap samples (and the mostly-fulfilled expectation that only winged specimens would be caught that way) may skew the result toward rejection of the null hypothesis by overestimating the real frequency of winged compared to wingless males. A more stringent test, therefore, can be made by reducing the influence of the flight intercept samples. This can be done in several ways; the  $\chi^2$  values and associated

Table 3. Chi-square tests of within-sex wing-morph frequencies of *O. flavidum* (using Yates' correction term for small expected numbers in one or more classes; see Sokal and Rohlf, 1969). Right column: maximum within-sex frequency of winged females (as a fraction of within-sex frequency of winged males) that does not require rejection of the null hypothesis that winged females exist.

	Null hypothesis: +W frequency in ♀ = +W frequency in ♂	Maximum +W♀ frequency as a fraction of +W♂ frequency
	$\chi^2$	P
1. # of specimens	115.08	<<<<0.001
2. # of specimens except those from flight intercept traps	11.15	<0.001
3. # of collections	23.41	<<0.001
4. # of collections except flight intercept traps	9.34	<0.005
5. # of specimens (flight intercept trap collections each counted as single specimen)	25.18	<<0.001

probabilities are given in Table 3 ( $\chi^2$  and P columns), lines 2–5, for several possible treatments of the data. Even with these manipulations, the equal-frequency null hypothesis is overwhelmingly rejected at the  $P = 0.05$  level.

An alternative class of null hypotheses can also be proposed: that winged females exist at a lower within-sex frequency than winged males. There are no obvious grounds for hypothesizing a particular ratio of female frequency to male frequency, but one can take an exploratory approach and calculate, under each method of counting the data (Table 3, lines 1–5), the highest frequency of winged females compared to winged males that could exist but be statistically indistinguishable ( $P \geq 0.05$ ) from the observed values. These threshold frequencies are given in the right-most column of Table 3. Such statistical explorations show that the existence of winged females cannot be ruled out completely; if such females do exist, however, they occur at a distinctly lower frequency than winged males. Flight timing of conspecific males and females is often different, so there would not necessarily be a concurrent peak abundance of the hypothetical +W females. The series of samples from West Lebanon, Maine (see Appendix B) further supports the non-existence of +W♀, as trapping before and after the +W♂ peak produced a few +W♂, but no females.

#### DISCUSSION

*Types and taxonomic distribution of dimorphism.* Wing dimorphism (sensu lato) including flightless and flying morphs is the central concern of this paper, rather than monomorphic aptery, microptery, or brachyptery. Not all variably-winged taxa show the same pattern of dimorphism, however. Of seven possible intraspecific patterns of variation in wing development with respect to sex, two are relatively common; the others seem to be much rarer and one is as yet unknown. Table 4 summarizes the higher-taxon placements of wing-dimorphic species reported in the literature, categorized by the wing condition in each sex. One of the two most common types

Table 4. Distribution of wing-dimorphisms with respect to sex; each taxon shown includes at least 1 species with the type of dimorphism indicated.

	+W♂
+W♀	<b>MONOMORPHICALLY +W SPECIES:</b> Most members of most orders of pterygote insects
±W♀	Homoptera: Aphididae [2,7] Hemiptera: Miridae [6] Hymenoptera: Bethylidae, Formicidae [2] Lepidoptera: Arctiidae, Geometridae, Lymantriidae, Pyralidae [8] Diptera: Sciaridae, Tipulidae [5]
-W♀	Embioptera [32] Phasmatodea: Phasmatidae [2] Orthoptera: Tettigoniidae [2] Blattodea: Blaberidae [2] Mantodea: Amorphoscelidae, Mantidae [2] Psocoptera [2] Homoptera: Coccoidea [2] Hemiptera: Microphysidae, Miridae [6] Strepsiptera [2] Coleoptera: Cerambycidae, Dascillidae, Elateridae, Lucanidae, Phengodidae (as Cantharidae), Scarabaeidae [31] Corylophidae, Drilidae, Lagriidae, Lampyridae, Meloidae, Ptinidae [17] Rhipiphoridae [2] Hymenoptera: Bethylidae, Cleptidae, Diapriidae, Dryinidae, Mutilidae, Sclerogibbidae [2] Lepidoptera: Arctiidae (s. l.), Gelechiidae, Geometridae, Hepialidae, Lasiocampidae, Lymantriidae, Megalopygidae, Momphidae, Noctuidae, Oecophoridae, Olethreutidae, Psychidae (and related families), Pyralidae, Symmocidae, Syntomidae, Tortricidae [8] Diptera: Cecidomyiidae, Chironomidae, Phoridae, Sciaridae, Tipulidae (some as Limoniidae) [5]

References: [1] Crowson (1981); [2] CSIRO (1970); [3] Kalmus (1945) (Agaonidae as Chalcidae); [4] Venturi (1964); [5] Hackman (1964); [6] Southwood & Leston (1959); [7] Hille Ris Lambers (1966); [8] Hackman (1966); [9] Darlington (1936); [10] Darlington (1943); [11] Lindroth (1979); [12] Den Boer *et al.* (1980); [13] Langor & Larson (1984); [14] Liebherr & Hajek (1986); [15] Desender (1989); [16] Shute (1980); [17] Jackson (1928); [18] Pope (1977); [19] Hammond (1985); [20] Paulian (1988); [21] Dybas (1978); [22] Taylor (1978; 1981);

Table 4 (continued). "-W" includes brachypterous, micropterous, and apterous. Numbers [x] indicate sources listed below; see Literature Cited for full references.

$\pm W\delta$	-W $\delta$
No examples found	Psocoptera [2] Thysanoptera [3] Coleoptera: Scolytidae [1] Hymenoptera: Agaonidae [2,3] Torymidae [2] Diptera: Sciaridae [4] Tipulidae (as Limoniidae) [5]
Orthoptera: Acrididae [2] Gryllidae, Pyrgomorphidae [26] Blattodea: Blaberidae [2] Isoptera [2] Zoraptera [2] Homoptera: Aphididae [2] Delphacidae [29] Hemiptera: Aradidae, Berytidae, Cimicidae, Dipsocoridae, Hebridae, Hydrometridae, Mesovelidae, Miridae, Nabidae, Pyrrhocoridae, Reduviidae, Rhopalidae, Saldidae, Tingidae, Veliidae [6] Gerridae [6,27] Lygaeidae [6,28] Thysanoptera [3] Coleoptera: Carabidae [9-15] Chrysomelidae [16] Cicindelidae, Curculionidae, Endomychidae, Hydrophilidae, Nitidulidae [17] Coccinellidae [18,19] Dermestidae [9] Dryopidae [20] Ptiliidae [21,22] Staphylinidae [19,23,24, this paper] Trogidae [25] Lepidoptera: Elachistidae, Gelechiidae, Noctuidae, Tineidae, Tortricidae, Yponomeutidae (as Hyponomeuthidae) [8] Diptera: Chloropidae, Sphaeroceridae (as Borboridae), Tipulidae [5] Sciaridae [30]	Psocoptera [3] Homoptera: Adelgidae, Pemphigidae [2] Thysanoptera [3] Diptera: Cecidomyiidae [5]
Embioptera [32] Homoptera: Aphididae [7] Coleoptera: Carabidae? [33] Dermestidae [34] Staphylinidae [this paper] Diptera: Sciaridae [5,35] Tipulidae (as Limoniidae) [5]	<b>MONOMORPHICALLY -W SPECIES:</b> Some members of most orders of neopterous insects

[23] Hammond (1979); [24] Campbell (1983); [25] Scholtz (1981); [26] Harrison (1980); [27] Vepsäläinen (1978); [28] Slater (1975; 1977); [29] Denno & Grissell (1979); [30] Steffan (1973; 1975); [31] Van Dyke (1933); [32] Ross (1970); [33] Liebherr (1989): *Tanystoma diabolica* may be  $\pm W\delta$ /-W $\delta$ ; it was described from only 5 specimens (2 +W $\delta$ , 1 -W $\delta$ , 2 -W $\delta$ ); [34] Barber (1947; 1948); [35] Steffan (1966).

is that in which both sexes show similar variation in wing development ( $\pm W\delta/\pm W\varphi$ ), although morph frequencies may differ between the sexes. Such non-sexual dimorphism has been recorded in some members of at least 49 families in ten orders (Table 4). Among these, Isoptera are a highly specialized case, with macropterous reproductives and apterous soldier and (in higher termites) worker castes occurring in both sexes.

The other commonest pattern of intraspecific wing variation is  $+W\delta/-W\varphi$ , one of the six types involving sexual dimorphism. This pattern occurs in all Strepsiptera (CSIRO, 1970), most Embioptera (Ross, 1970), and in some members of at least 49 families in 11 other orders.

Other sex-related patterns of wing variation appear to be distinctly rarer than these two, especially among Coleoptera. The pattern of  $+W\delta/\pm W\varphi$  has been reported in at least ten families in five orders (Table 4). Most species of Formicidae (Hymenoptera) can be regarded as a special case of this category, having two or more female castes ( $+W$  reproductives,  $-W$  workers and sometimes soldiers) and only  $+W$  males. Aphididae (Homoptera) (Hille Ris Lambers, 1966) and Lymantriidae and Pyralidae (both Lepidoptera) show seasonal (generation-to-generation) rather than simultaneous (within-generation) dimorphism (Hackman, 1966).

I found no reports of species that are  $\pm W\delta/+W\varphi$ , and only a few (in four orders) that are  $-W\delta/\pm W\varphi$ . Species with the pattern  $-W\delta/+W\varphi$ , in at least seven families in five orders, include Agaonidae (Hymenoptera) (Kalmus, 1945, as Chalcididae; CSIRO, 1970) and some of the Torymidae (Hymenoptera) that parasitize them (CSIRO, 1970).

The pattern of primary interest in this paper is the also rare one of  $\pm W\delta/-W\varphi$ . This pattern has been reported previously in four orders (see Table 4), mostly in a single species per family. Discovery of this pattern in *Omalium flavidum* Hamilton provides the first case of this (and in fact any) pattern of sexual wing dimorphism in Staphylinidae.

*Associated morphological changes.* Various morphological changes beyond lack of wings are commonly associated with the evolution of flightlessness in insects. Coleoptera, with their front wings modified into elytra and related specializations of thoracic structure, have diverged significantly from other insects in general body organization. Many modifications accompanying wing loss in Coleoptera thus have no close parallel in other orders, and the following discussion deals principally with Coleoptera.

The most extreme modifications are generally found in monomorphically brachypterous species, particularly those belonging to entirely flightless lineages. In the latter cases flight capability presumably was lost in a temporally rather distant ancestor of any extant species, allowing more time for development of other modifications than would be expected for a wingless species having all fully-winged relatives. At its fullest development (short of reduction to a larviform morph), what could be called a "flightless beetle syndrome" includes: loss of wings and flight muscles (direct and indirect); rounding of elytral humeri; tighter than normal locking, or even fusion (ankylosis), of the elytra to each other; reduction in length and width of the metathorax; reduction in elytral length (sometimes to tiny vestiges); loss of abdominal wing-folding and wing-toiletry devices (Hammond, 1979, 1985); reduction in dorsal sclerotization of the pterothorax and (except in brachelytrous forms, e.g., Staphylin-

idae and Meloidae: *Meloe*) abdomen; reduction in size of spiracles of abdominal segment 1 (Rüschkamp, 1927; Jackson, 1956); loss of eyes; and sometimes (depending at least partly on microhabitat) reduction in antennal length and/or body pigmentation. Within a number of insect orders, ocelli are sometimes reduced or lost along with wings (Kalmus, 1945). Very atypically for Coleoptera, most Omaliinae (Staphylinidae) have ocelli, but no correlation of wing and ocellar loss has yet been found in this group.

Jackson (1928) found no external differences between macropterous and brachypterous individuals of *Sitona hispidula* (Curculionidae). The brachypterous morphs of many other wing-dimorphic species of Coleoptera (also Lygaeidae [Hemiptera]; Slater, 1977) do, however, exhibit some features of the "flightless beetle syndrome" despite normal development of the corresponding features in macropterous conspecifics. A few examples from Coleoptera follow. Reduction of eyes in wingless morphs, reported here in *O. flavidum*, has also been reported in *Aglyptinus dimorphicus* (Leiodidae, Peck, 1978), *Leistus americanus* (Carabidae, Darlington, 1936), and species of the genus *Ptinellodes* (Ptiliidae, Dybas, 1978). The last-named also show reduction of elytra in the wingless morph ("vestigial morph" of Dybas, 1978), as do *Platystethus nitens* (Staphylinidae, Hammond, 1985) and *Omalium flavidum* (reported here). Reduction of the elytral humeri occurs in wingless morphs of *Trox* spp. (Trogidae, Scholtz, 1981), *Pseudomacronychus* spp. (Dryopidae, Paulian, 1988), *O. flavidum*, and rarely in dimorphic Carabidae (though commonly in monomorphically -W species; Darlington, 1936). Reduction in metathoracic size has been found in wingless morphs of *Platystethus nitens* (Staphylinidae, Hammond, 1985) and *Tanystoma maculicolle* (Carabidae, Liebherr and Hajek, 1986) as well as *O. flavidum*, while reduction in dorsal meso- and metathoracic sclerotization occurs in *Sitona hispidula* (without reduction in size; Curculionidae, Jackson, 1928) as well as *O. flavidum*. Reduction in size of the spiracles of abdominal tergite 1 seems not to have been reported previously in dimorphic beetle species, but occurs in -W males of *O. flavidum*.

Discussion of the state of flight muscles is seldom part of normal taxonomic work, but in special studies of the subject, reduction or loss of these muscles in wingless and some winged individuals has been found in *Sitona hispidula* (Curculionidae, Jackson, 1928), *Bembidion lampros* (Carabidae, Langor and Larson, 1984), and several other species of Carabidae (Den Boer et al., 1980). In many cases (including some monomorphically macropterous species discussed by Den Boer et al., 1980), there is seasonal change in development of flight muscles in individuals. Undoubtedly more such examples will be found when more species are investigated in this regard. Fusion of elytra seems not to have been recorded in dimorphic Coleoptera, although Lindroth (1949) mentioned two species of Carabidae in which some brachypterous individuals show a slight amount of fusion.

Two features of the "flightless beetle syndrome" that are quite rare in wingless morphs of dimorphic species are loss of abdominal wing-folding patches and loss of "palisade" or "wing-toiletry" fringes (Hammond, 1979). Hammond (1985) surveyed over 300 species of wing-dimorphic beetles in several families and found (in addition to *Ptinellodes* spp., Dybas, 1978) only one, *Rhyzobius litura* (Coccinellidae), dimorphic in presence of wing-folding patches and only *R. litura* and some species of *Othius* and *Mycetophorus* (both Staphylinidae) dimorphic in presence of the palisade fringe.

*Glypholoma rotundulum* (Staphylinidae: Omaliinae) is dimorphic in the size, not presence, of its wing-folding patches (Thayer, unpublished). *Omalium flavidum*, as reported here, provides an additional example of dimorphism in each of these features (see above and Appendix A), although the distributions of the reductions are not concordant. This non-concordance runs counter to the sometimes-observed pattern of morphological changes associated with wing loss apparently evolving in a certain sequence (at least within a given lineage), yielding a nested pattern of losses (Jeannel, 1926; Hammond, 1979; Scholtz, 1981).

*Mechanisms producing and maintaining wing dimorphism.* Roff (1986a, b) reviewed mechanisms of wing length determination; the number of species whose wing-determination has been studied in detail is still extremely small. At least many cases of wing dimorphism are what Clark (1976) called "genetically determined polymorphism" (Roff [1986a, b] and Roff and Fairbairn [1991] cited a total of 29 examples). Sequential wing dimorphism (e.g., seasonal changes in many aphids: Hille Ris Lambers, 1966; Lees, 1966; Clark, 1976; MacKay et al., 1983) and some cases of non-seasonal dimorphism appear, on the other hand, to be largely what Clark termed "environmentally cued polymorphism," in which environmental factors interact with the genotype to produce different morphs under different conditions. Such a mechanism was suggested by Dybas (1978) for some Ptiliidae and by Denno and Grissell (1979) for a species of Delphacidae (Homoptera). There can also be genetic variation in presence or thresholds of environmental response (Vepsäläinen, 1978; Denno and Grissell, 1979). Morph determination in individuals is probably hormonally mediated, possibly by levels of juvenile hormone (Southwood, 1961; Wigglesworth, 1961; Roff, 1986a, b).

Even where genetic control of wing morphs occurs, there appears to be variation in its nature. In the 29 examples cited by Roff and Fairbairn (1991) and Roff (1986a, b), single-locus systems are more common in holometabolous orders and polygenic systems far more common in paurometabolous orders. Roff (1986b) argued that even if wing dimorphism arose in a species as a single-locus mutation, selection would favor replacement of single-locus control by a system of polygenic control because of the greater flexibility of polygenic systems in responding to environmental fluctuations. Roff (1990a) and Roff and Fairbairn (1991) gave evidence for the occurrence of antagonistic pleiotropy in maintenance of wing dimorphism in *Gryllus firmus* (Orthoptera) (and potentially in other species) in the form of a tradeoff between migration ability and earlier age at reproduction. The contention in the former work, however, that "expression of wing form . . . in . . . wing dimorphic insects in general, is highly dependent on environmental conditions such as temperature and photoperiod . . ." appears to be based almost entirely on paurometabolous insects (e.g., Honek, 1976, 42 paurometabolous, 5 holometabolous species). Roff and Fairbairn (1991), in contrast, said ". . . the available evidence suggests a genetic basis [for wing dimorphism] in most species. . . ." The seeming difference between holometabolous and paurometabolous insects in the type of genetic control of wing polymorphism and the still-limited data bearing on the question leave the importance of environmental conditions to morph determination in Holometabola uncertain.

I have found no explicit discussions of the genetic or non-genetic basis of sexually dimorphic wing development; Roff (1986a) listed two species of Aphididae (Homoptera) as having polygenic wing morph determination, but did not specifically

discuss sexual wing dimorphism. Work done on sexual dimorphism of wing development in aphids (e.g., Lees, 1966; MacKay et al., 1983) suggests that determination of morphs in female aphids is under complex environmental control. Determination of wing morphs in male aphids has been studied far less, and it is not clear whether it is produced by genetic or environmental factors (or both). In any case, the extreme complexity of aphid life cycles leaves some question as to how applicable the aphid results are to other insects.

*Ecology and evolution of wing loss.* On the basis of observed occurrences and theoretical considerations, various workers have summarized or predicted conditions under which brachyptery is favored, including: small-area stable ("permanent") habitats (Darlington, 1943; Vepsäläinen, 1978), including those on mountains (Darlington, 1943; Scholtz, 1981); isolated habitats (in combination with stability and areal limitation; Lindroth, 1949; Vepsäläinen, 1978); cold areas or seasons of activity (Downes, 1965; Byers, 1969); caves (Jeannel, 1926; for different reasons, Barr, 1968); and areas providing distinctly suboptimal conditions for a species (Jeannel, 1926, but with little or no support from other workers). It is also well known that many nidicolous or parasitic insects are wingless (e.g., Arixeniina and Hemimerina [Dermoptera]; Phthiraptera [loss of wings probably preceded parasitism; Lyal, 1985]; Cimicidae and Polycenidae [Hemiptera]; Staphylinidae: Amblyopinini and Leiodidae: Platypsyllinae [Coleoptera]; Siphonaptera; Nycteribiidae, Hippoboscidae, and Streblidae [Diptera]). Hackman (1964) attributed most cases of wing loss in Diptera (aside from halobionts and parasites) to the adults' living in "concealed terricolous habitats" (including galleries of social insects), where he suggested selection might favor morphological changes improving the ability to run, even at the expense of the ability to fly. The unusual groundplan of Coleoptera, with the flight wings protected by elytra, facilitates the coexistence of good running and flying abilities and presumably would reduce selective pressure against flight in microhabitats with restricted passageways. Wing loss does appear to be less common in litter-dwelling Coleoptera than Diptera, although soil-inhabiting beetles are more likely to be wingless (e.g., Coiffait, 1960).

Roff (1990b) judged available data to be consistent with the idea of habitat stability favoring evolution of flightlessness, but not yet adequate to test the importance of other potential factors such as temperature or physical constraints. Barbosa et al. (1989) argued convincingly that habitat stability alone may not be a sufficient explanation for evolution of brachyptery or wing dimorphism; the way in which a species interacts with its habitat may also play a key role.

In contrast to the idea of strongly directional selection for brachyptery in stable environments, Hamilton and May (1977) demonstrated that even in relatively unchanging habitats an evolutionarily stable strategy (ESS) is likely to include a significant probability of migration of offspring from the parent's "unitary site" (individual site occupied by one individual in the model). Although these authors mentioned the relevance of their models to insect species having flying males and flightless or flight-dimorphic females, they did not discuss the key relationship between unitary site size and capability of dispersal by means other than flight. How large is an insect's unitary site? In a species whose individuals can move beyond their natal unitary site by walking, swimming, or larval ballooning (Barbosa et al., 1989), even complete loss of flight capability would not preclude an ESS involving significant probability

of dispersal. This potential nonidentity of flight capability and dispersal/migration ability, admittedly difficult to investigate, is often overlooked in discussions of wing and flight loss.

Reasons for the origin, persistence, and spread of wing loss remain somewhat uncertain and may well vary among species. Although Jeannel suggested "senility" of lineages (1926) or inheritance of changes caused directly by effects of cave environments (1943), there seems little reason to doubt that random mutations are the underlying cause of wing loss. Darlington (1936) suggested that wing atrophy arises through spontaneous mutations (occurring persistently at a significant rate), and might in some cases increase through simple accumulation of the mutations in the absence of natural selection against wing loss. On the other hand, it seems likely that natural selection could often be involved, whenever advantages of winglessness (or flightlessness) outweigh selective pressures favoring flight. Both flight and the synthesis of muscle and other tissues needed for it are energetically expensive (Roff and Fairbairn, 1991 and references therein). Wingless forms, by rechanneling this biosynthetic and locomotory energy into earlier or greater total reproduction, might gain a substantial fitness advantage over +W forms under circumstances where flight was not essential (Darlington, 1936, 1943; Byers, 1969; Dybas, 1978; Roff and Fairbairn, 1991; but not Taylor, 1978). (Evidence for such an "energy conservation hypothesis" in bacterial systems is mixed [Zamenhof and Eichhorn, 1967; Dykhuizen, 1978].) In contrast, Regal's (1977) "noise suppression theory" proposes that natural selection favors loss of non-essential structures because such elimination removes informational noise (thus potential errors) from the process of transcription of the genome.

Wing dimorphism has been predicted to occur when the habitat (or microhabitat) of a species is mostly stable with occasional disruptions (Darlington, 1936; Southwood, 1962; Hammond, 1985; Roff, 1986a). When a species has different habitat requirements at different times of year, the selective advantage of dispersing may vary seasonally (Cohen, 1967); under such conditions, sequential wing dimorphism may be favored in bi- or multivoltine species (Harrison, 1980). Some authors (e.g., Lindroth, 1949; Den Boer et al., 1980; Roff and Fairbairn, 1991) have regarded wing dimorphism or polymorphism as an intermediate state in the transition to brachyptery, in essence predicting that dimorphic species should be found in the same situations as monomorphically brachypterous ones, but in habitat patches that have been stable a shorter time than those with brachypterous species.

There has been relatively little discussion of possible reasons for sex-biased wing dimorphism. Downes (1965) and Byers (1969) suggested that in the Arctic the severe energetic demands of the climate have caused selection for a +W♂/-W♀ pattern. The short available reproductive season there makes it advantageous for females to produce their eggs as soon as possible after emerging in the spring; the resulting extra weight of mature eggs would make female flight energetically very expensive, perhaps impossible. In a number of arctic species, therefore, females appear to have maximized their reproductive effort by abandoning flight ability and males have specialized in mate location and dispersal by flight, the latter permitting outcrossing. (Some other arctic species have instead abandoned outcrossing or even mating.) Such arguments may apply equally well to cold montane areas at lower latitudes.

Other circumstances associated with the pattern of +W♂/-W♀ are: (1) in some

Hymenoptera, adaptations for burrowing (or host-seeking behavior in other tight places) by females and transport of therefore  $-W$  females by males (CSIRO, 1970) and (2) in some eastern North American forest Lepidoptera, a complex of life-history traits including polyphagy on dominant trees with common chemical defenses, univoltinism, larval ballooning, and overwintering as eggs or larvae (Barbosa et al., 1989). Clearly neither these nor the cold hypothesis provides a general explanation for sexual wing dimorphism, but all three point out the complex connections between such dimorphism and life-history traits.

Roff and Fairbairn (1991) found reproductive advantages of brachyptery for females, but not males. This inequality may, in fact, be one factor behind the relative commonness of  $+W\delta/-W\varphi$  species. Evolution of such dimorphism would, of course, depend on preexistence of a suitably modifiable genetic control system. Given that sex determination is usually chromosomal, it seems possible that a locus on one of the sex chromosomes might modify the effects of a somatic allele for brachyptery to produce various kinds of sex-linked patterns of dimorphism.

*How does Omalium flavidum fit in?* *Omalium flavidum* is one of the few insect species known to have  $\pm W$  males and  $-W$  females, and is the first such species recorded in the large and biologically diverse beetle family Staphylinidae.

*Omalium flavidum* is unusual among wing-dimorphic beetle species in exhibiting dimorphism of two wing-associated abdominal structures (palisade fringe and tergal wing-folding patches). Hammond (1979, 1985) found only a few cases of variability in one or both of these structures in wing-dimorphic beetle species; in those cases, the  $+W$  morph retained and the  $-W$  morph lacked the structure in question. *Glypholoma rotundulum*, mentioned above, has reduced wing-folding patches in the micropterous morph (see below). In *O. flavidum*, the loss of wing-folding patches is fully correlated with wing loss, but the palisade fringe is lost only in females (see Table 1). The tergite 3 groove usually present in winged (but not wingless) species of Omaliini is vestigial in females and both male morphs.

The patterns of variation found in *O. flavidum* differ from the other cases of wing-variation known so far in Omaliinae in being sexually dimorphic and apparently geographically undifferentiated. *Glypholoma rotundulum* was described (Thayer and Newton, 1979) from southeastern Australia on the basis of over 200 micropterous (there called "brachypterous") males and females from several sites, plus 2 truly brachypterous individuals (1 ♂, 1 ♀) and 1 macropterous ♂ from the two (very close) northernmost sites. Based on the type series and additional material I have seen (including macropterous males and females from the same and two additional localities; Thayer, unpublished), tests like those in Table 3 support the hypothesis that fully-winged individuals occur at the same (low) frequency in both sexes of *G. rotundulum*. The abdominal wing-folding patches are dimorphic in this species, being larger in macropters and brachypters than in micropters. Brachypterous and macropterous individuals of this species are still known only from the northernmost localities for the species and the micropterous form, universal elsewhere, has not been collected at those sites. Hammond (1985) mentioned wing dimorphism in four other species of Omaliinae, none of which appears to be sexually wing-dimorphic. Three of these (*Olophrum fuscum* (Gravenhorst), *Eucnecosum* (as *Arpedium*) *brachypterum* (Gravenhorst), and *Acidota cruentata* Mannerheim), with macropters rare to very rare,

have the wing-folding patches monomorphic and smaller than those of related macropterous species. The fourth, *Anthobium unicolor*, has varying frequencies of macropters over its range; Hammond did not discuss its wing-associated structures.

There is also a slightly odd pattern of abdominal spiracle size in *O. flavidum*. All morphs have the spiracles of segment 1 larger than those of segments 2 and 3, which are in turn larger than those of segment 4; this seems to be the normal configuration in at least Omaliini (Thayer, unpublished) and probably a much wider group. The spiracles on segments 1–3 of macropterous males are larger than the corresponding ones of –W males (Figs. 4, 6, 21 vs. 5, 7, 22). Winged species of Omaliini similarly have larger spiracles 1–3 than do wingless species, and such a difference has also been found between +W and –W species in Chrysomelidae (Rüschkamp, 1927) and Dytiscidae (Jackson, 1956). The (–W) females of *O. flavidum* also have larger spiracles than –W♂, however. This could reflect higher oxygen needs of egg production compared to sperm production, or perhaps greater locomotory activity among females than –W males. I have not seen a sex-based difference in spiracle size in wingless species of Omaliini, and neither Rüschkamp (1927) nor Jackson (1956) mentioned any differences between the sexes in this regard. Divergence in spiracle size may be greatly underreported, however, since (like wing-muscle development) it is not a character usually examined in taxonomic work.

As discussed earlier, wing dimorphism has been shown to be variously genetically or environmentally controlled (or a combination) in different species. From the limited data available, it appears that in Coleoptera (as in other Holometabola) it is usually genetically determined (Roff, 1986a). In the absence of any rearing data or evidence regarding seasonal change in morph frequencies, it is impossible to say how wing dimorphism is determined in *O. flavidum*. If there are indeed no +W females, the mechanism in this species is clearly not a simple single-locus, two-allele, autosomal genetic system with brachyptery dominant, like that found in several species of Coleoptera (Carabidae, Curculionidae) and Diptera (Sphaeroceridae) cited by Roff (1986a). Two possibilities are: (1) some form of direct genetic sex-linkage or (2) sex-determined effects on hormonal mediation of wing development, with females reacting in one way and males in either of two ways.

Most previously reported ±W♂/–W♀ species have male morphs that are at least partly sympatric (Dermestidae: *Thylodrias contractus*, Barber, 1947; Sciaridae [Diptera]: *Pnyxia scabiei*, Hackman, 1964; some Embioptera, CSIRO, 1970; but not Tipulidae [Diptera]: *Pedicia hannai*, Hackman, 1964; Byers, 1969). Not all known *O. flavidum* localities are represented by specimens of all morphs (or even both sexes), but both male wing morphs are widely distributed over the range of the species; no clinal variation in occurrence vs. latitude is evident (Fig. 1), in contrast to numerous species mentioned by Roff (1990b). There is no other obvious pattern of geographical restriction, and the two male wing morphs have been collected together at four sites so far; *O. flavidum* is thus not unusual among ±W♂/–W♀ species in the geographical distribution of its male morphs.

The driving force favoring evolution of wing dimorphism in *Omalium flavidum* (or brachyptery, if its dimorphism is a transitional stage) is not yet clear, perhaps in part because of the limited ecological data available. As mentioned above, the species inhabits the widespread eastern North American deciduous and deciduous-coniferous forests. Before the widespread forest clearing that accompanied European settlement,

this climax forest biome had a far more continuous distribution than it does now. This would have provided large areas of relatively unbroken favorable habitat for *O. flavidum*, presumably with scattered areas of disturbance caused by severe storms or occasional treefalls. Several authors (Southwood, 1962; Harrison, 1980; Hammond, 1985; Roff, 1986a) have suggested that conditions such as these favor evolution (in both sexes) of either wing-dimorphism or brachyptery, depending on the level of habitat stability. Could bisexual dimorphism be a stage that *Omalius flavidum* has already passed through, en route to brachyptery? Such a pathway to brachyptery can be envisioned: under conditions allowing brachyptery, if the energy conservation hypothesis is valid, stronger (hence faster) selection for wing loss in females than males might occur because of the greater reproductive investment by females than males. If this were the case, however, one would expect wing dimorphisms like that of *O. flavidum* to be far more common.

On an ecological time scale, the eastern forests have constituted a relatively stable habitat for a long time; their stability, however, does not extend very far back on a geological scale. All but the southernmost records of *O. flavidum* (southern Pennsylvania, District of Columbia vicinity) are from areas that were ice-covered during the Pleistocene glaciations (Fig. 1; Flint, 1971; Morgan and Morgan, 1981). Thus, the eastern forests only came to occupy a large part of the present range of *O. flavidum* during the last 8,000–10,000 years (Matthews, 1979), presumably moving in from the south (and/or east, if the continental shelf formed a glacial refugium; Flint, 1971). Obviously, stable forest did not appear immediately behind the disappearing glaciers, so the time available for colonization by mature-forest inhabitants such as *O. flavidum* would have been even less.

When did wing loss develop in *O. flavidum*? Three alternatives can be proposed if the wing loss is assumed to be a result of habitat stability. First, if wing loss developed independently in many newly established local populations as a result of relatively stable habitats, one would expect to find a distribution pattern like that of *Calathus mollis* (Carabidae) in Scandinavia (Lindroth, 1979), with brachypterous forms predominating in the longest-occupied (southern) areas. No such pattern is apparent in the data available for *O. flavidum*, so this appears not to be the explanation. Second, if dimorphism arose only after *O. flavidum* had fully occupied more or less its present range, the phenomenon would not necessarily occur throughout the species' range, and morph frequencies might be expected to vary more or less randomly over space. Multiple population samples (taken throughout the year) would be needed to test this hypothesis; the data now available for *O. flavidum* are far too scanty for such purposes. Finally, the species might already have had its present form of wing-dimorphism while in a glacial refugium and when the ice sheet began to retreat, managed to disperse over a large area despite the flightlessness of females. Although this seems absurd at first glance, over a period of 8,000 years it would require movement on the order of 100 m per year, which might be possible. (Morgan and Morgan, 1981, arrived at a similar conclusion for a flightless species of Carabidae.)

Alternatively, *O. flavidum*'s seasonal pattern of occurrence, seeming to reflect a preference for (adaptation to?) cool to cold conditions, and the (partly) sexual nature of its dimorphism, suggest that wing-dimorphism in this species might be an example of a cold-adaptation pattern such as discussed above (Downes, 1965; Byers, 1969).

Further knowledge of the distribution and seasonality of the species, study of larger samples of multiple populations, investigation of the genetic basis of its wing dimorphism, and more detailed information about its habits and microhabitat may help to clarify the factors involved in the evolution of the unusual wing dimorphism found in *Omalium flavidum*. Understanding this case might also help to elucidate the reasons for the evolution of a similar pattern in other taxa and for the rarity of this pattern.

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#### APPENDIX A

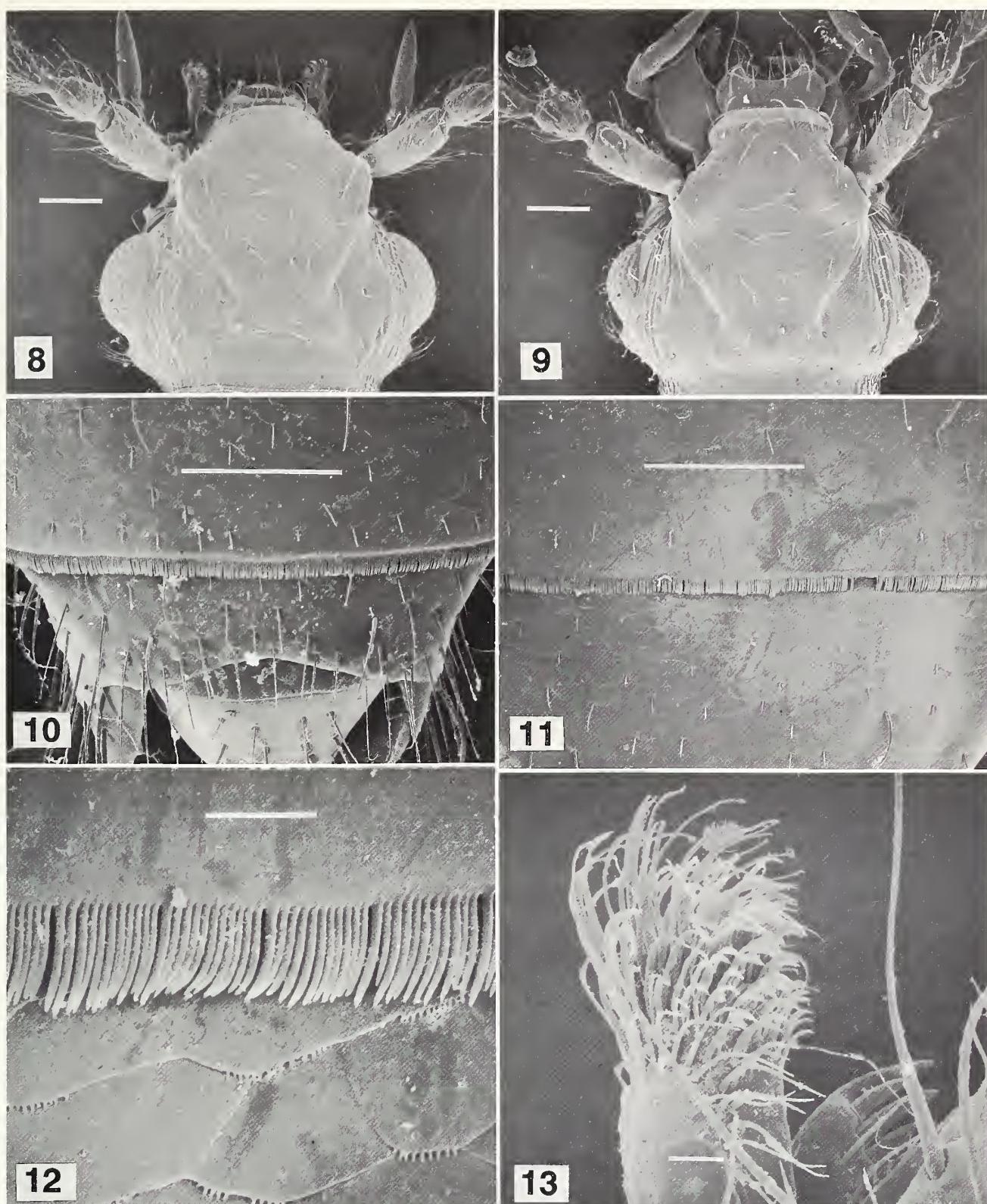
##### Redescription of "*Omalium*" *flavidum* Hamilton and Lectotype Designation

*Redescription.* Yellowish- or reddish-brown to dark brown, varying among morphs (see Table 1). Body sparsely punctate and sparsely setose (Figs. 4, 5); dorsal surfaces of head (except neck), pronotum, and elytra without microsculpture; abdomen with reticulate microsculpture of varying distinctness.

Head (Figs. 8, 9) with pair of ocelli on vertex, often concolorous with surrounding cuticle (thus difficult to see); head width 1.2–1.3 × head length; distinct neck present; frontal area elevated, delimited posteriorly by oblique ridges running from behind antennal bases to just in front of ocelli; eyes well-developed (somewhat reduced in  $-W\delta$  and ♀), with seta-fringed ridge posterior to each eye (Figs. 8, 9); cuticle above and behind eye with curved ridges roughly paralleling margin of eye; gular sutures close but not confluent between eyes, diverging posteriorly. Labral apex arcuately emarginate; epipharynx with sensilla and setae arranged as in Figure 14. Mandibles apically acute, asymmetrical, each with well-developed articulated mola bearing vertical ridges on adoral surface; ventral surface of each mandible near middle with band of mostly apically bifid setae running from anterolateral to posteromedial; right mandible with a single sharp preapical tooth, left with a blade-like preapical area. Galea (Fig. 13) with densely setose apex; lacinia with medial comb of spine-like setae and unarticulated apical spine (Fig. 13); maxillary palp with 4 articles, all but first subequal in maximum width, ultimate about 2.5 × as long as penultimate (Figs. 8, 9). Labial palp of 3 articles subequal in width, the ultimate longest, penultimate shortest. Antenna 11-segmented, without distinct club, longer than head and pronotum together (length varying among morphs: see Tables 1, 2); with dense long blunt sensilla on antennomeres 3–11 in  $\delta$ , 5–11 only (and concentrated at apices) in ♀;  $+W\delta$  with all antennomeres longer than wide, ♀ and  $-W\delta$  with antennomeres 1–3 and 11 longer than wide, 6–10 wider than long, and 4–5 quadrate or slightly wider than long; antennomere 3 slightly wider in  $-W\delta$  than in ♀.

Pronotum (Figs. 4, 5) slightly transverse, width about 1.25 × length, widest slightly anterior to middle, narrowed slightly sinuately from there toward base; lateral margins narrowly explanate; disc with raised roughly triangular median area enclosing longitudinal impressions on either side of midline.

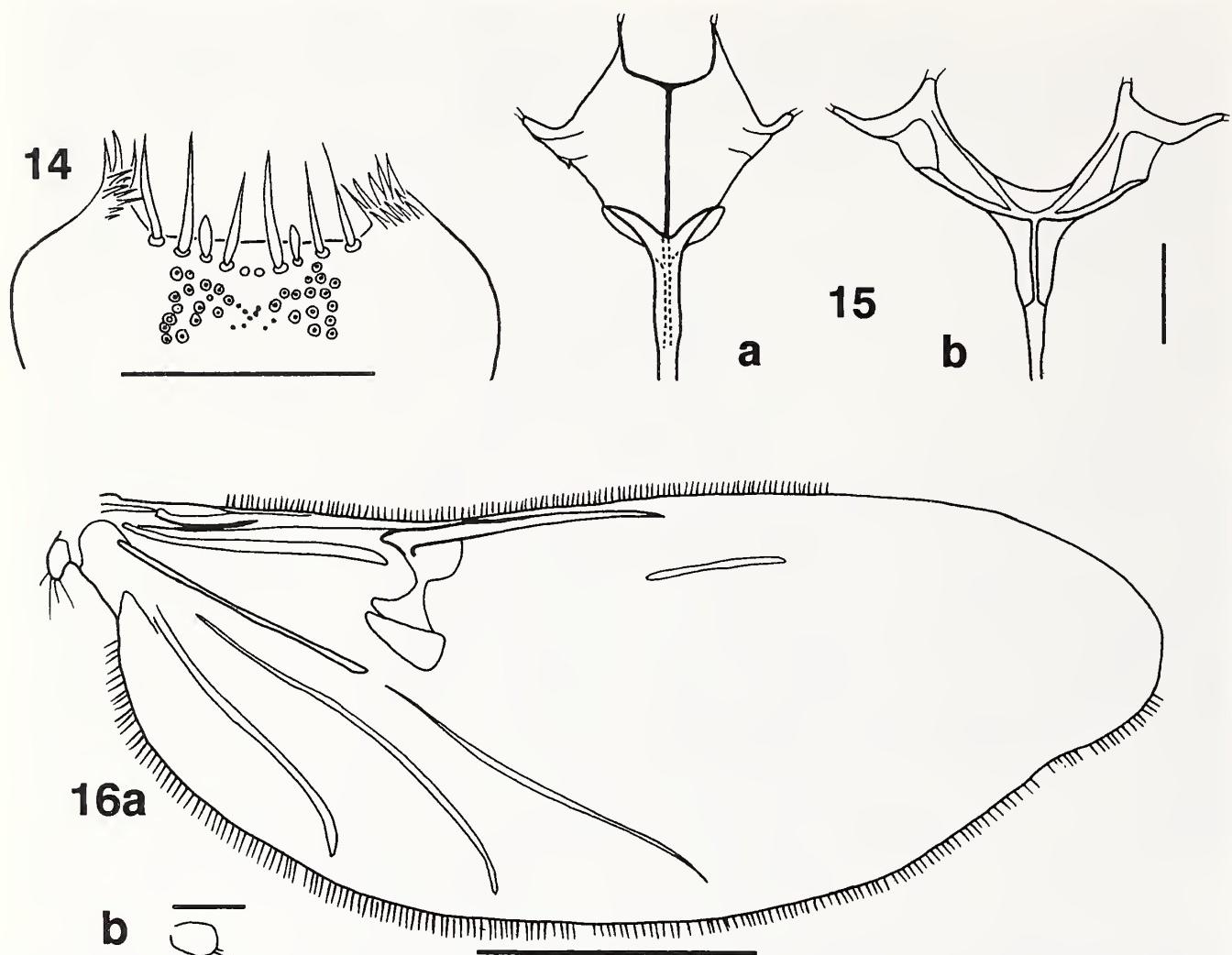
Elytra of  $+W\delta$  loosely interlocked, with arcuate apices, length about 1.5 times conjoint width and nearly 3 times as long as pronotum, covering part or all of abdominal tergite 5, humeri prominent; of ♀ and  $-W\delta$  very tightly interlocked (though not fused), with truncate apices, about as long as their conjoint width and about 1.5 times as long as pronotum, only covering tergite 3, humeri reduced and rounded. Mesosternum not carinate. Metathorax of  $+W\delta$  (Fig. 6) normal in size (Fig. 2a, Table 1) and sclerotization, normal flight muscles present, metendosternite as in Figure



Figs. 8–13. *Omalium flavidum* Hamilton. 8. Head, dorsal view, +W♂. 9. Same, -W♂. 10. Median area of abdominal tergite 7 apex, +W♂. 11. Same, -W♂. 12. Detail of 11. 13. Apex of left galea, +W♂, dorsal view. (Scale line: Figs. 8–11, 100  $\mu$ m; Figs. 12–13, 10  $\mu$ m.)

15a; metathorax of ♀ and -W♂ (Fig. 7) reduced in length (Fig. 2a, Table 1), width, and dorsal sclerotization, without flight muscles, metendosternite as in Figure 15b. Wings normally developed (+W♂, Fig. 16a) or minute (♀, -W♂, Fig. 16b).

Tarsi 5-segmented; empodium bisetose, one seta much longer than other (Fig. 19);



Figs. 14–16. *Omalium flavidum* Hamilton. Scale lines = 0.1 mm, except in Fig. 16a, 1 mm. 14. Epipharynx, ♀, ventral view. 15. Metendosternite, dorsal view. (a) + W $\delta$ ; (b) - W $\delta$ . Right wing, dorsal view. (a) + W $\delta$ ; (b) - W $\delta$ .

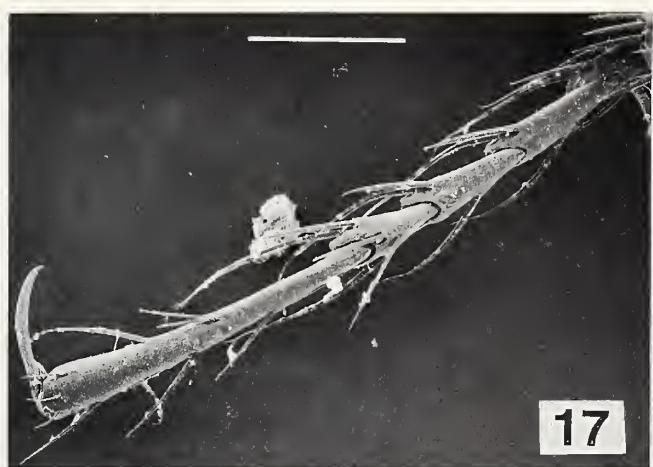
+ W $\delta$  with hind tarsus (Figs. 2b, 17) about two-thirds as long as hind tibia, tarsomeres 1–4 together longer than 5 (Fig. 2c, Table 1), ♀ and - W $\delta$  with hind tarsus (Figs. 2b, 18) no more than 0.6 as long as hind tibia, tarsomeres 1–4 together shorter than 5 (Fig. 2c, Table 1).

Abdomen with spiracles on segments 1–8, located in tergite of segments 3–7, in membrane adjacent to tergite of segments 1–2 and 8; spiracles 1–3 distinctly (♀, + W $\delta$ ) or slightly (- W $\delta$ ) larger than following ones; one pair of paratergites on each of segments 3–7; intersegmental membranes connecting segments 3–7 bearing brick-

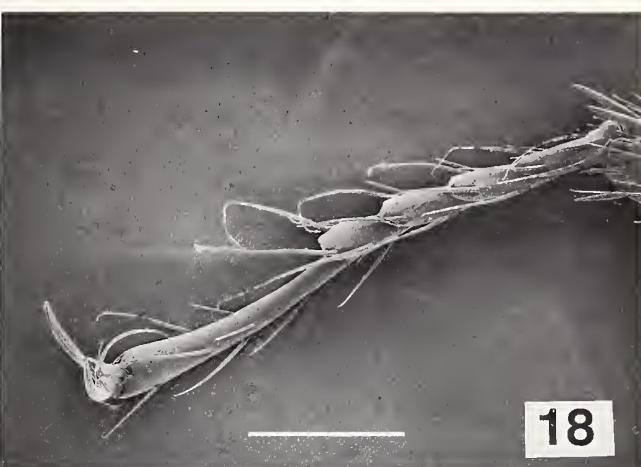
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Figs. 17–20. *Omalium flavidum* Hamilton, tarsi. 17. Hind tarsus, + W $\delta$ , dorsal view. 18. Same, - W $\delta$ , oblique ventral view. 19. Detail of 18, showing unequal empodial setae. 20. Front tarsus, - W $\delta$ , dorsal view. (Scale line: Figs. 17–18, 20, 100  $\mu$ m; Fig. 19, 25  $\mu$ m.)

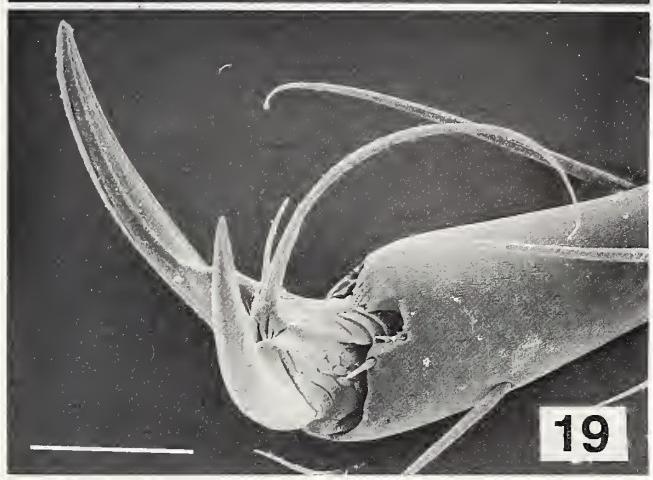
Figs. 21–24. *Omalium flavidum* Hamilton, abdominal tergites. 21. Tergite 3, with arrow indicating vestigial row of setae near apex, + W $\delta$ . 22. Same, - W $\delta$ . 23. Tergites 4 and 5, + W $\delta$ . 24. Same, - W $\delta$ . (Scale line: Figs. 21–22, 100  $\mu$ m; Figs. 23–24, 200  $\mu$ m.)



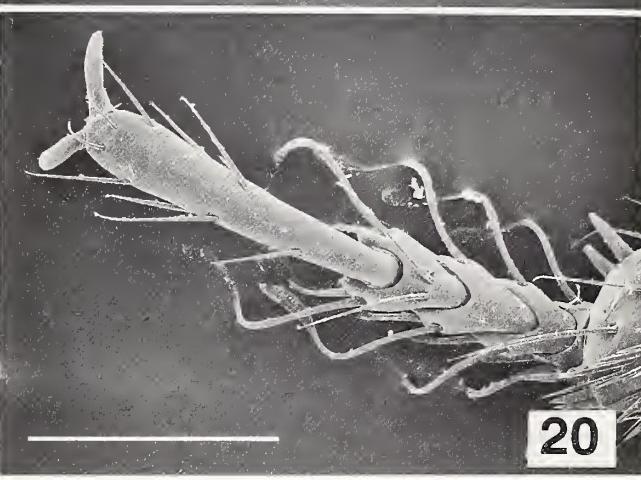
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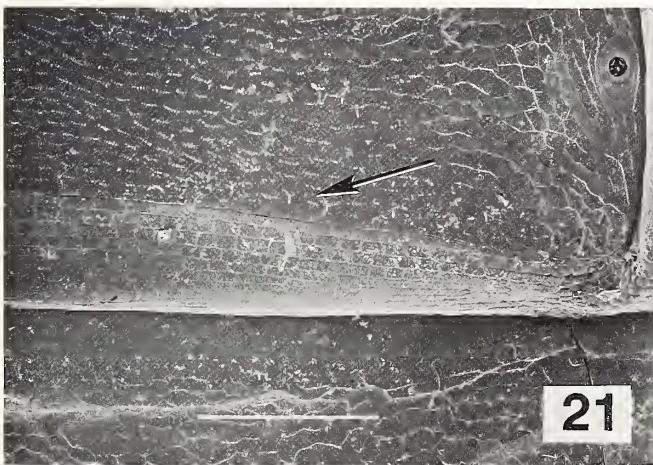
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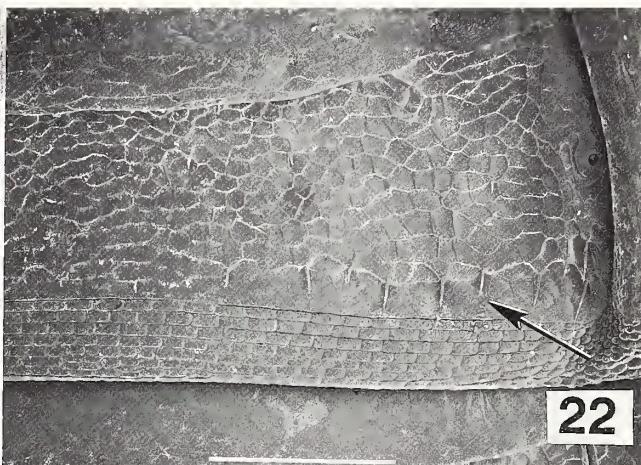
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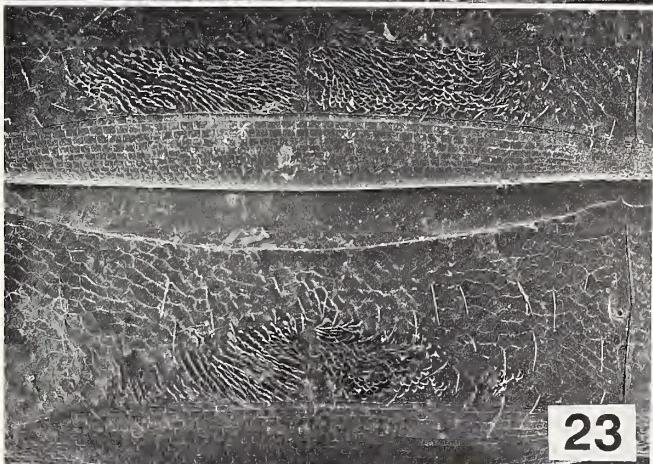
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Figs. 25, 26. *Omalium flavidum* Hamilton, abdominal sternites. 25. Sternites 7 and 8, -W $\delta$ , ventral view. 26. Anterior median projection of sternite 8 with associated gland tubules, +W $\delta$ , ventral view. (Scale line: 0.1 mm.)

wall pattern of sclerites (Figs. 21–24); tergite 3 posteriorly with vestiges of transverse seta-edged groove (Figs. 21, 22); sternite 3 with distinct hind coxal impressions delimited by a ridge; wing-folding patches present on tergites 4–5 of +W $\delta$  only (Fig. 24, cf. Fig. 23); tergite 7 with ( $\pm$ W $\delta$ , Figs. 10–12) or without (♀) apical palisade fringe; sternite 8 with anterior projection bearing ducts of defensive gland cells (Fig. 26).

**Male.** Front tarsus with tenent setae on tarsomeres 1–4 (Fig. 20). Sternites 7 and 8 with characteristic arrangement of short stout setae apically (Fig. 25); genital segment (Fig. 27) with tergite 9 continuous across dorsum. Parameres of aedeagus dorsal when aedeagus is retracted within abdomen; aedeagus as in Fig. 28, with small thin basal piece, median lobe with median desclerotized band at base and on abparameral side, and internal sac with complex armature of small spines and sclerotized plates.

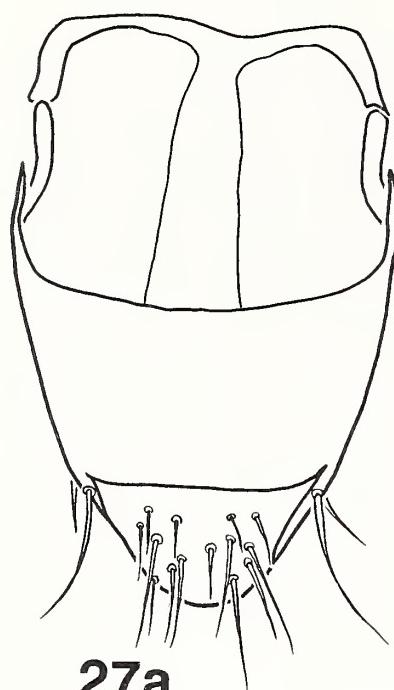
**Female.** External genitalia (Fig. 29) lacking sternite 9; tergite 9 divided dorsally; tergite 10, two pairs of gonocoxites, and one pair of styli present; lightly sclerotized structure present internally, extending anteriorly from tergites 9 and 10 when genitalia are extended, including a flat portion in median sagittal plane and small pale oval “window” in horizontal plane on each side of it, near anterior end (Fig. 29, broken lines). Spermatheca (Fig. 30) lightly sclerotized, two-chambered.

**Lectotype designation.** Hamilton (1896) stated that “several examples occurred near St. Vincent.” His collection is at the Carnegie Museum, which houses two apparent syntypes of *O. flavidum*. I here designate as lectotype the intact female, bearing the labels: St. Vinc. Penn./type/Carn. Mus. Acc. 349/[blank red label]/LECTOTYPE *Omalium flavidum* Hamilton des. M. K. Thayer 1991. I designate the male (-W morph, abdomen missing) a paralectotype; its labels read: St. Vinc. Penn./Carn. Mus. Acc. 349/PARALECTOTYPE *Omalium flavidum* Hamilton des. M. K. Thayer 1991.

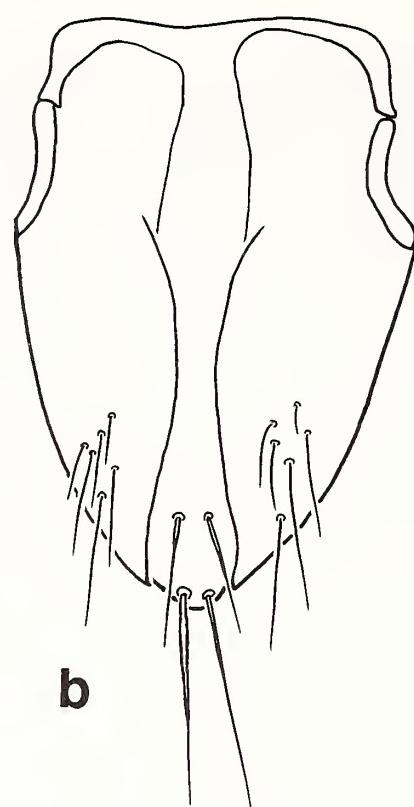
## APPENDIX B

## Material Examined (all ♀ are -W)

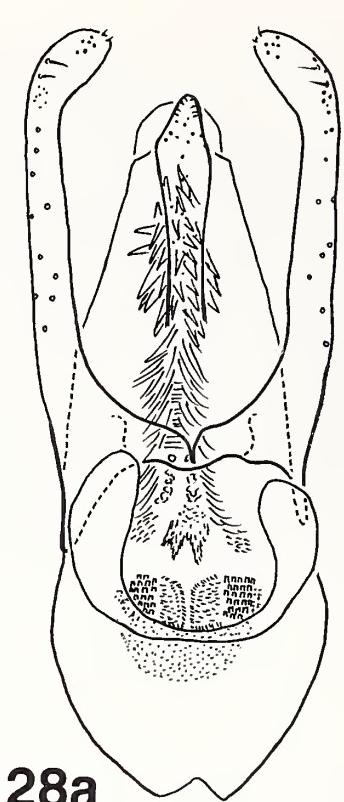
**Canada:** ONTARIO: 2♂ (-W), 3♀, Chaffeys Locks, birch-maple litter beside logs, 23.x.1985 (A. Davies) (CNC); 1♂ (+W), Kemptville, intercept, 25.x-8.xi.1983 (L. Dumouchel and J. Denis) (CNC); QUÉBEC: 1♂ (-W), Johnville, TP-066, 4.v.1988 (C. Levesque) (CNC). **United States:** DISTRICT OF COLUMBIA: [no locality], 1♂ (-W) (CM); MAINE: Androscoggin Co.: 1♂ (+W), Poland Spring, 27.xi.1909 (JHE) (MCZ); York Co.: 5♂ (+W), West Lebanon, 20-29.xi.90, FIT, disturbed forest (DW Barry) (UNH); 3♂ (+W), West Lebanon, FIT, disturbed forest, 30.xi-5.xii.90 (DW Barry) (UNH); 20♂ (+W), West Lebanon, FIT, disturbed forest, 11-17.xii.90 (DW Barry) (UNH); 16♂ (+W), West Lebanon, FIT, disturbed forest, 18-26.xii.90 (DW Barry) (UNH); 1♂ (+W), West Lebanon, FIT, disturbed forest, 27.xii.90-7.i.91 (DW Barry) (UNH); 2♂ (+W), West Lebanon, FIT, disturbed forest, 6-12.ii.91 (DW Barry) (UNH); 2♂ (+W), West Lebanon, FIT, disturbed forest, 15-24.iii.91 (DW Barry) (UNH); 1♂ (+W), West Lebanon, FIT, disturbed forest, 25-31.iii.91 (DW Barry) (UNH); MARYLAND: Prince Georges Co.: 1♂ (+W), Takoma Pk., 3 mi E, flying, 17.xii.1949 (G. H. Nelson) (GHN); MASSACHUSETTS: Hampshire Co.: 1♂ (-W), Northampton, 14.xi.1917 (CNC); Middlesex Co.: 1♀, Framingham, sifting, 17.xi.1934 (C. A. Frost) (MCZ); 3♂ (2 +W, 1 -W), 1♀, Tyngsboro, 17.xi.1901 (MCZ); 1♀, Tyngsboro, 3.xi.1915 (MCZ); 1♂ (-W), Tyngsboro, sifting leaves, 7.xi.1924 (MCZ); NEW HAMPSHIRE: Carroll Co.: 3♂ (-W), 1♀, Passaconaway Cpgd., spruce-fir-pine-hwd., 340 m, leaf and rain-washed litter, berl., 17-18.x.1973 (A. Newton) (ANMT); 1♀, Passaconaway Cpgd., spruce-fir-pine-hwd., 340 m, leaf and rain-washed litter, berl., 15.x.1978 (A. Newton and M. Thayer) (ANMT); 1♂ (+W), The Bowl, 2.5 mi NW Wonalancet, 590 m, FIT, 20.x-7.xi.1984 (D. S. Chandler) (UNH); 1♂ (-W), The Bowl, 2.5 mi NW Wonalancet, 590 m, sift birch log, 1.xi.1984 (D.S. Chandler) (CNC); 1♀, The Bowl, 2.5 mi NW Wonalancet, 590 m, sift conifer logs, 17.x.1985 (D. S. Chandler) (UNH); 1♂ (-W), The Bowl, 2.5 mi NW Wonalancet, 590 m, sift birch logs, 31.x.1985 (D. S. Chandler) (UNH); 30♂ (28 +W, 2 -W), The Bowl, 2.5 mi NW Wonalancet, 590 m, FIT, 1-19.xi.1985 (D. S. Chandler) (UNH); 3♂ (2 +W, 1 -W), The Bowl, 2.5 mi NW Wonalancet, 590 m, on snow, 19.xi.1985 (D. S. Chandler) (UNH; CNC); Coos Co.: 1♂ (-W), Mt. Washington toll rd, 0.3 mi below Halfway Hse., spruce-fir-birch for., 1100 m, litter, berl., 15.x.1978 (A. Newton and M. Thayer) (ANMT); Grafton Co.: 1♀, Franconia, 26.xii.1960 (K. W. Cooper) (USNM); 1♀, Hubbard Brook Exp. For., Bear Brook, 460 m, sift rotten wood, 15.x.1982 (D. S. Chandler) (UNH); 3♂ (-W), 3♀, Kancamagus Pass, spruce-fir-birch, 850 m, litter, berl., 19.x.1973 (A. Newton) (ANMT); 1♀, Kancamagus Pass, spruce-fir-birch, 850 m, litter, berl., 15.x.1978 (A. Newton and M. Thayer) (ANMT); Strafford Co.: 5♂ (+W), Durham, 1 mi SW, FIT, 15.x-4.xi.1987 (D. S. Chandler) (UNH); 2♂ (1 +W, 1 -W), Durham, 1 mi SW, FIT, 18.xi-4.xii.1987 (D. S. Chandler) (UNH); 15♂ (14 +W, 1 -W), Spruce Hole, 3 mi SW Durham, FIT, 5-24.xi.1987 (D. S. Chandler) (UNH; CNC); 6♂ (+W), Spruce Hole, 3 mi SW Durham, FIT, 4-15.xii.1987 (D. S. Chandler) (UNH); NEW YORK: St. Lawrence Co.: 1♀, Wanakena [as Wananeke], 15.x.1982 (Lee Herman) (AMNH); Tompkins Co.: 1♂ (+W), Caroline, on snow, 12.iii.1963 (M. A. Deyrup) (AMNH); 1♂ (+W), Ithaca, 10.iv.1926 (Fletsher) (CU); 1♀, Jacksonville, N, maple+ forest, dead maple buttress, FMHD #82-49, 24.v.1982 (W. S. Suter) (FMNH); PENNSYLVANIA: 1♀, [state only] (CM); Philadelphia Co.:



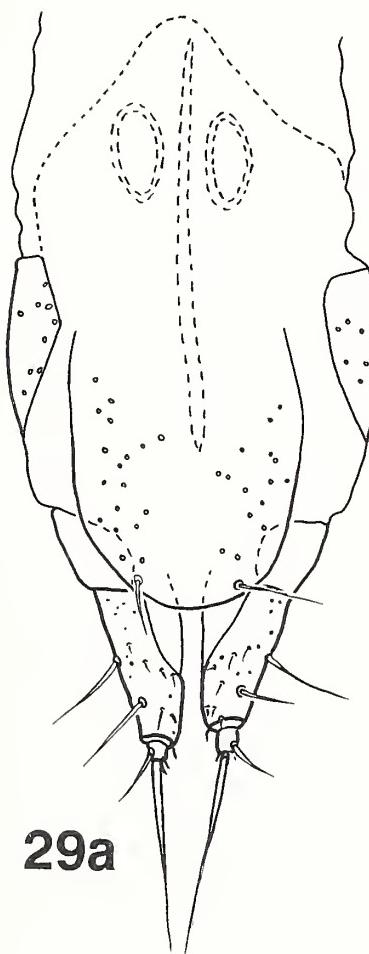
27a



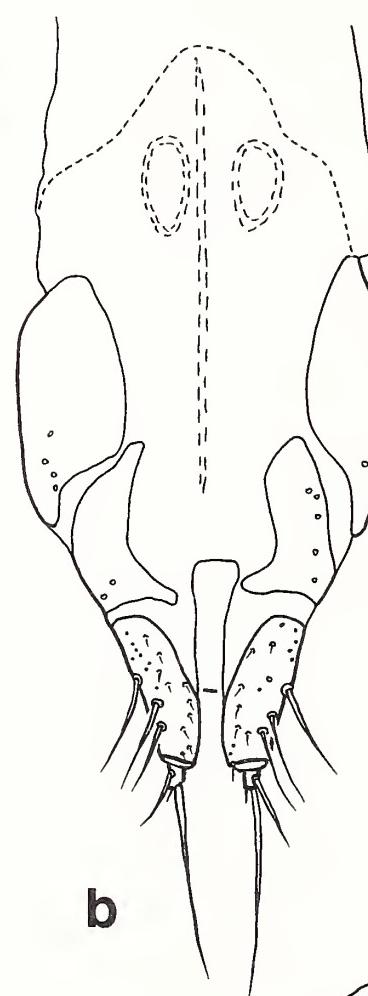
b



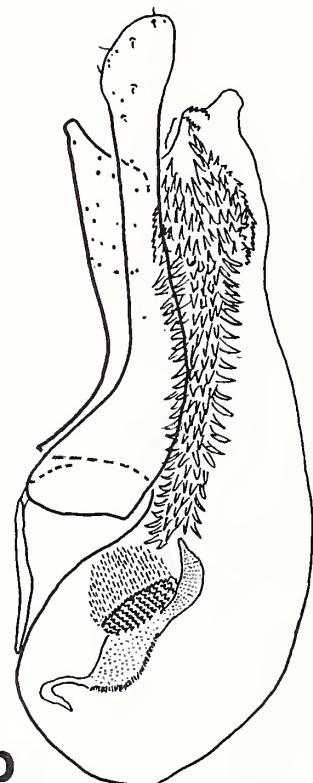
28a



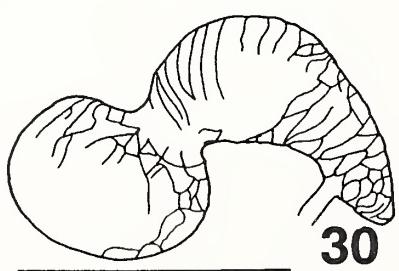
29a



b



b



30

1♂ (−W), Manayunk [as Manyunk], 5.x (J. W. Green colln.) (CAS); Schuylkill Co.: 1♂ (+W), Pottsville, forest, trap #203, 1–11.iv.1967 (S. Peck) (FMNH); Westmoreland Co.: 1♀, Jeannette, x (H. G. Klages) (CM); 1♀, Jeannette, xii (H. G. Klages) (CM); 1♀, Jeannette, "VIII.16" (H. G. Klages) (CM); 1♂ (+W), Powdermill Nature Res., nr Rector, cabins area on snow, 25.ii.1958 (CM; CM Acc. 18464); 1♂ (−W) (Paralecotype), 1♀ (Lectotype), St. Vincent [as St. Vinc.] (CM).

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Figs. 27–30. *Omalium flavidum* Hamilton. Scale lines = 0.1 mm. 27. Male genital segment (segments 9–10), +W. (a) dorsal view; (b) ventral view. 28. Aedeagus. (a) −W♂, parameral view (dorsal in repose); (b) +W♂, lateral view. 29. Female external genitalia, anterior broken lines indicating lightly sclerotized internal sclerite. (a) dorsal view; (b) ventral view. 30. Spermatheca (spermathecal gland attached to subapical duct not shown).

## TWO NEW SPECIES OF DIPLOTAXIS FROM MEXICO (COLEOPTERA: MELOLONTHIDAE)

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*Abstract.*—Two new Mexican species of *Diplotaxis* from Veracruz state are described. Modifications to Vaurie's keys to the genus are included to allow their identification.

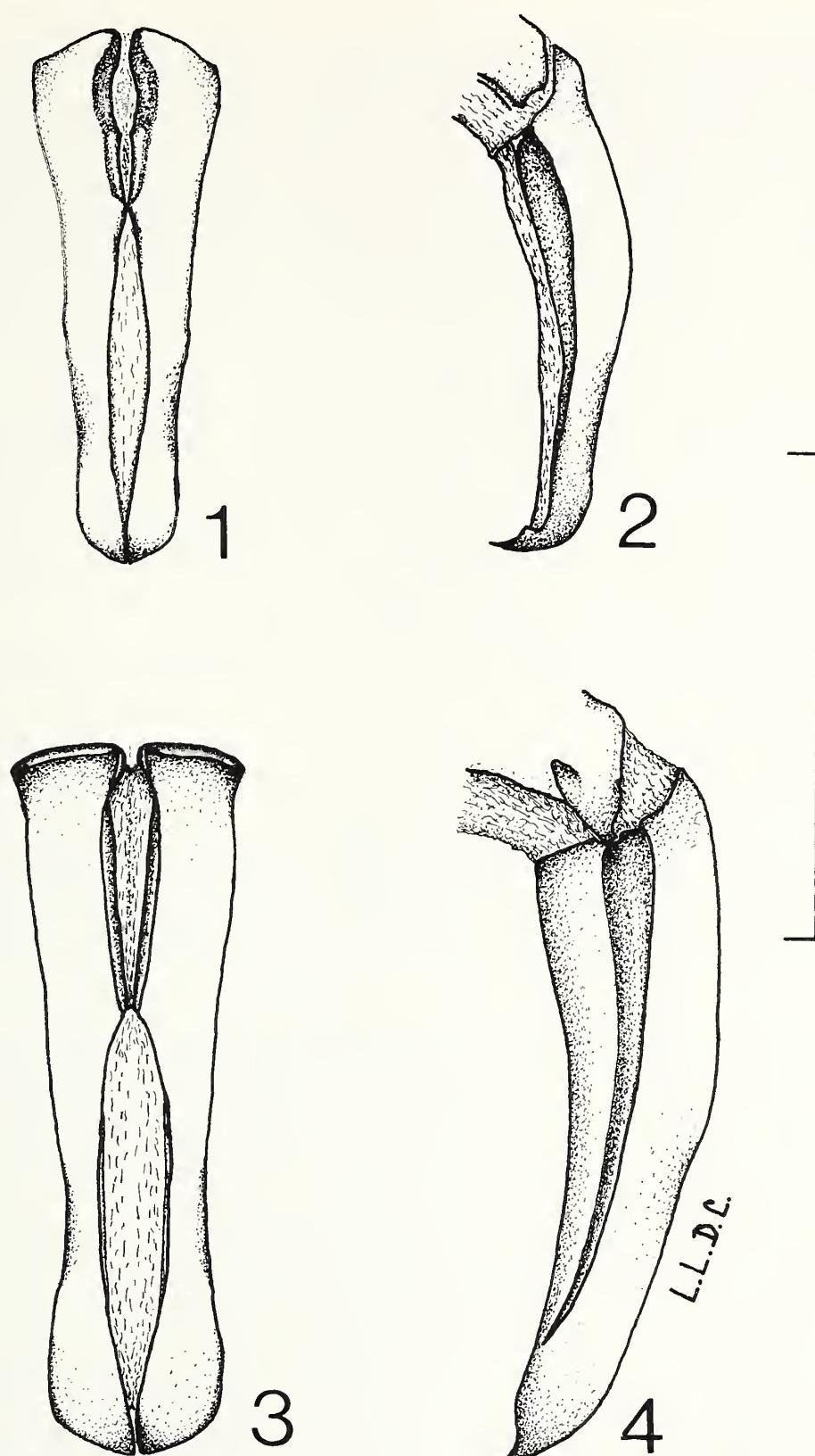
The American genus *Diplotaxis* includes 221 species, most of which (about 77%) are distributed in Mexico (Vaurie, 1958, 1960, 1962; Delgado-Castillo, 1990). However, only 18 species have been cited from Veracruz state: six are localized in the lowland tropical rain forest with four of these six extending their distribution to Central America; five others occur principally in areas above 1,500 m; two others are distributed almost exclusively in the cloud forest (one of which, *D. veracruzana* Vaurie, is a Veracruz endemic); and five others with various habitat preferences (*D. aenea* Blanchard, *D. angustula* Moser, *D. atramentaria* Bates, *D. coriacea* Bates and *D. puberea* Bates) seem to be very scarce in Veracruz and need to be confirmed.

In this paper we describe two new species from Veracruz state, and incorporate them into Vaurie's keys.

### **Diplotaxis xalapensis, new species** (Figs. 1–2)

*Type material.* Holotype ♂, labeled: “MEXICO, Veracruz, Xalapa, Rancho Guadalupe, Km 2.5 Antigua carr. a Coatepec. Bosque mesófilo–cafetal. Alt. 1,360 m, Luz. 13-II-1991. L. Delgado, col.” Allotype ♀ labeled as holotype, except: 6-7-III-1992, F. Capistrán, J.R. Hernández y L. Delgado, cols. Paratypes 54 ♂♂, 29 ♀♀. One male labeled as holotype. 32 ♂♂, 21 ♀♀ labeled as allotype. 17 ♂♂, 8 ♀♀ labeled as holotype except: 8-III-1991 (1♂), 14-III-1991, L. Arellano, col. (4♂♂); 8-IV-1991 (1♂); 10-III-92, P. Rojas, col. (1♂); 20-III-92, F. Capistrán y E. Santos, Cols. (10♂♂, 7♀♀). 4 ♂♂ labeled: “MEXICO, Veracruz, Xalapa, Briones, Alt. 1,360 m. 28-III-1991. M.A. Morón, col.” One female labeled Mexico: Veracruz, 2 km al NE de Calcahuasco. AH. 1,650 m Bosque mesófilo 4-V-92 a la luz, Capistrán y Delgado, cols.

Holotype and four paratypes deposited at the Instituto de Biología–Universidad Nacional Autónoma de México (Mexico City), paratypes deposited at the following collections: British Museum Natural History (London), Muséum National d’Histoire Naturelle (Paris), Zoologisches Museum Humboldt Universität (Berlin), Canadian National Collection (Ontario), United States National Museum (Washington), American Museum of Natural History (New York), Museu de Zoologia da Universidade de São Paulo, Museu Nacional da Universidade Federal do Rio de Janeiro, Universidad Nacional de Venezuela (Maracay), Museo Argentino de Ciencias Naturales (Buenos Aires), Laboratorio Natural Las Joyas–Universidad de Guadalajara (Jalisco),



Figs. 1–4. New species of *Diplotaxis*. 1–2. *D. xalapensis* 1. Parameres, frontal view. 2. Parameres, lateral view. 3–4. *D. squamisetis*. 3. Parameres, frontal view. 4. Parameres, lateral view. Scale = 1 mm.

Museo de Historia Natural de la Ciudad de México, Instituto de Ecología (Veracruz), M. Bunalski (Poznan), H. & A. Howden (Ontario), B. D. Gill (Ontario), B. C. Ratcliffe (Nebraska), W. B. Warner (Arizona), S. McCleve (Arizona), P. K. Lago (Mississippi), A. A. De Ascencao (Merida), A. Martínez (Salta), G. Halfster (Veracruz), M. A.

Morón (Veracruz), J. Blackaller (Mexico City), J. R. Hernández (Veracruz), F. Capistrán (Veracruz) and L. Delgado (Mexico City).

*Description.* Holotype male. Length 7.2 mm; elytral maximum width 3.0 mm. Body elongate and flattened; front of head, disc of pronotum, abdomen and pygidium metallic green; elytra opaque green, sericeous; clypeus, marginal regions of pronotum and scutellum brilliant reddish; venter and legs yellowish-red. Clypeus trapezoidal, as long as the front, with obtuse front angles, broadly emarginate anteriorly and sides indented in front of eyes; surface deeply concave, except for a tumid small central area; some short setae present only behind the margins and with scarce, minute setae on disc; fronto-clypeal suture well marked and sinuate at middle; clypeal surface densely rugose. Front with anterior half abruptly descending to clypeus, with scarce medium-sized punctures and concave at central region, posterior half flattened and with rugose punctuation; transverse eye diameter almost  $0.25 \times$  as wide as head. Antenna 10-jointed. Labrum slightly concave with dense punctures, level with and  $0.75 \times$  the length of the reflexed underside of clypeus; mandibles slender; mentum slightly convex, with anterior declivity marked by transverse sharp, setiferous ridge; last article of maxillary palpus not impressed dorsally.

Pronotum hexagonal; fore angles acute, lateral angles obtuse and situated nearly at the middle, hind angles obtuse; pronotal surface with longitudinal mesial furrow and four irregular depressions each side of midline as follows: one on anterolateral corner, one lateral, one on posterolateral corner and one central, last two larger than the others; pronotal surface irregularly elevated with large punctures, some of them confluent, the punctuation between them becoming finely reticulate to marginal regions; pronotum laterally and basally with cariniform, narrow margin, with the adjacent region depressed, basal margin crenate. Scutellum with scarce medium-sized punctures.

Elytra longer than wide (1:0.66), with irregular rugose swellings, many of them branching off from convex costae; punctures smaller than those on pronotum, irregularly placed and with scarce, minute setae overall (only visible at high magnification); striae not evident, except the two outer ones; marginal setae scarce and very short, present only on basal quarter. Abdomen laterally rounded; propygidium not grooved above pygidium; abdominal sternites 1–5 subequal in length, with long setae more abundant laterally; pygidium wider than long and with coarse and deep punctures, some confluent, and with setae more or less abundant, those on apical half longer.

Protibiae tridentate, basal tooth scarcely marked and situated in the distal half; claws slightly curved, cleft subapically, tooth entire and shorter than apex; tarsi longer than respective tibiae; basal mesotarsomere almost as long as second one; metacoxal plates margined laterally and truncate; metafemora straight and slender; metatibial spurs slender, long and acute; basal metatarsomere shorter than the second one and of the same length as the longest spur.

Genitalia with basal piece a little longer than parameres, which are jointed on inner margin at basal third and abruptly bent at the apex (Figs. 1–2).

Allotype female. Length 7.5 mm; elytral maximum width 3.2 mm. Differs from holotype in the following respects: elytra with metallic reflections; clypeus with only the marginal regions yellowish-red, a little shorter than the front, scarcely reflexed, the anterior margin truncate and the front angles rounded, half posterior of the front a little convex and with punctures not confluent; transverse eye diameter  $0.20 \times$  as

wide as head; labrum as long as the underside of clypeus; last article of maxillary palpus shorter; pronotum with fore angles almost right, with the surface almost evenly elevated, with punctures not confluent and the reticulated punctuation reduced; fifth abdominal sternite shorter than each sternites 1–4; pygidium with coarser and deeper punctures almost crater-like; femora wider and robust; protibia wider and with the basal tooth clearly marked, meso and metatibiae more flared out at apex; metatibial spurs wider; protarsi shorter; basal metatarsomere shorter than the longest spur; claws shorter, tooth of the same length as the apex, obliquely truncate and more separated from the apex.

*Variation.* Males, length: 5.8–7.7 mm, elytral maximum width: 2.6–3.5 mm; females, length 6.1–7.7 mm, elytral maximum width 2.7–3.6 mm. In the males the color of elytra is generally sericeous green; and in the females metallic-green; the brilliant reddish color on the marginal regions of clypeus and pronotum varies a little in extent. Setae on clypeus, scutellum and elytra varies from more or less abundant to nearly absent; pygidial punctures vary in density and depth; length of the basal metatarsomere varies from a little longer to shorter than the longest metatibial spur. The shape of clypeus, the transverse eye diameter, the length of labrum, the last article of palpus maxillary, the pronotal fore angles and the legs are considered dimorphic characters.

*Type locality.* Km 2.5 Antigua carr. a Coatepec, Rancho Guadalupe, Xalapa, Veracruz, Mexico.

*Remarks.* *D. xalapensis* presents most of characters given by Vaurie (1960:191) to the “Trapezifera” group as: clypeus hairy (only behind front edge), eye large, antennae 10-jointed, mandibles small, elytra about three times longer than the pronotum, abdomen not ridged laterally, propygidium without groove, metacoxal plates margined laterally and not angulate, and basal tooth of protibiae in the distal half. However *D. xalapensis* shows characters not shared with other species of this group, such as the unevenly elevated dorsal surface, the hexagonal shape of pronotum, and the elytral punctuation and microsculpture with a metallic or sericeous cast, which give it an unusual and distinctive appearance, and the shape of the claws.

A species that shows the same elytral punctuation and microsculpture is *D. aurata* Bates, which differs from *D. xalapensis* by the labrum longer than underside of clypeus, the pronotum arcuate near middle, and the elytra with long, erect setae. We key out *D. xalapensis* in the “trapezifera” group for convenience, however, this species seems not to have close affinities to this group. Rather it shows possible relationships with *D. aurata*, a species only cited from Guatemala.

*D. xalapensis* is an early flying species, and this phenology could explain why it has not been collected before, since the area has been visited by many entomologists over a long time.

*Etymology.* This species is dedicated to the City of Xalapa de Enríquez, where it was collected, and one of the classical localities of the faunal work “Biología Centrali-Americana.”

The key to the “trapezifera” group proposed by Vaurie (1960:193), is modified as follows to incorporate *D. xalapensis*:

- 27 Pronotum with sides strongly arcuate behind middle and hind angles rounded off without angulation; side margins of clypeus almost parallel to front; Guerrero, Puebla ..... *incisa*

- 27' Pronotum with sides scarcely arcuate or angulate, and hind angles distinctly angulate; side margins of clypeus converging obliquely to front; Durango, (Hidalgo?), Veracruz ..... 27a
- 27a Color wholly light red; clypeus with dentiform front angles; elytral striae clearly distinguished; Durango, (Hidalgo?) ..... *saltensis*
- 27a' Color of the elytra and the most of the pronotum and front green, marginal regions of clypeus reddish; clypeus with obtuse or rounded front angles; striae of the elytral disc not distinguished; Veracruz ..... *xalapensis*

**Diplotaxis squamisetis, new species**  
(Figs. 3-4)

*Type material.* Holotype ♂, labeled: "MEXICO: Veracruz, Los Tuxtlas, Sierra de Santa Marta, Ocotal Chico. 17-18-VII-1982. Alt. 700 m, colecta nocturna. H. Pérez, col." Allotype ♀, labeled: "MEXICO: Veracruz, Catemaco, Pipiapan, Parque de la Flora y Fauna Silvestre Tropical. 16-IV-91. Alt. 600 m, selva mediana perennifolia/comiendo hojas de *Guarea glabra* (Meliaceae). O. Aquino y F. Capistrán, cols." Paratypes 6♂♂, 1♀. 2♂♂ labeled as holotype; 1♀ labeled as allotype, except: "13-15-IV-1991. Luz ultravioleta. G. Cabrera y F. Capistrán, cols"; 4♂♂ labeled: "MEXICO: Veracruz, Estación Biología "Los Tuxtlas," 250', V-20-1983/ C.W. & L. O'Brien & G.B. Marshall."

Holotype and allotype deposited at the Instituto de Biología, Universidad Nacional Autónoma de México (Mexico City). Paratypes deposited at the following collections: W. B. Warner (Arizona), S. McCleve (Arizona), M. A. Morón (Veracruz), F. Capistrán (Veracruz) and L. Delgado (Mexico City).

*Description.* Holotype male. Length 9.3 mm, elytral maximum width 4.6 mm. Body ovate, robust, reddish-brown, densely clothed with yellowish scale-like setae. Clypeus rectangular, its length nearly equal to  $0.33 \times$  the cephalic length, slightly and broadly emarginate in front and with the fore angles rounded; punctation large and dense with erect scale-like setae. Fronto-clypeal suture without setae, except at center; frons with punctation similar to that of clypeus but with longer and semierect setae; transverse eye diameter equal to  $0.25 \times$  the cephalic width. Labrum twice longer than underside of clypeus and with dense, fine punctures; mandibles robust; mentum almost flat, with lateral depressions posteriorly and with anterior declivity little marked. Antennae 10-jointed, club reddish; last article of the maxillary palpi not impressed.

Pronotum evenly rounded laterally, wider at middle, fore and hind angles obtuse; pronotal surface with dense setiferous punctures, setae erect directed to midline, surface between the punctures finely punctate; anterior margin with long, erect setae; posterior margin with short, decumbent setae. Scutellum densely punctate and with decumbent setae overall.

Elytra longer than wide (1:0.70); punctation similar to that of pronotum; striae little evident; elytral surface with setae shorter than the length of scutellum, most of them decumbent; some erect setae on the costae and sutural interval. Abdomen ridged laterally; propygidium not grooved; abdominal sternites of equal length, clothed with decumbent setae and with a transverse row of erect setae; pygidium a little wider than long, densely punctate-setiferous, setae long semierect and short decumbent.

Protibiae tridentate, teeth placed in the distal half, basal tooth slightly marked; protarsi shorter than protibiae; mesotarsi longer than mesotibiae; first and second mesotarsomere of same size; basal metatarsomere of same length as the longest metatibial spur; claws abruptly bent and subapically cleft, tooth wider than the apex but of the same length and with distal half broadly separated from the apex. Genitalia with basal piece a little longer than parameres, which are jointed behind the middle and widened on apical third (Figs. 3–4).

Allotype female. Length 9.1 mm; elytral maximum width 4.9 mm. Differs from holotype in the following respects: pygidium a little longer and the basal metatarsomere shorter than longest metatibial spur.

*Variation.* Female, length 8.6 mm; elytral maximum width 4.5 mm. Males, length 6.8–8.4 mm; elytral maximum width 3.4–4.3 mm. The color of the elytra varies from reddish-brown to reddish, the density of the setae varies a little, possibly by abrasion, and the apex of clypeus is almost truncate in the smaller specimens.

*Type locality.* Ocotal Chico, Sierra de Santa Marta, Los Tuxtlas, Mexico.

*Remarks.* *Diplotaxis squamisetis* does not fit into any presently defined groups of the genus. The presence of dense vestiture over all of the body, formed by decumbent, semierect and erect yellowish scale-like hairs is exclusive to this species, and very different from all other setiferous species of *Diplotaxis*, as the species of the “puberula,” “pilipennis” and “pilifera” groups. In the first two groups the vestiture is formed by erect and fine setae and in the last one by white, short, scale-like setae apressed to the surface. Other species with thick scaly vestiture are *D. clypeata* Bates and *D. mus* Fall, the former differing principally from *D. squamisetis* by the smaller eyes, dark antennal club, lack of pubescence on elytral striae, shape of clypeus and different vestiture (similar to that of the “pilifera” group); the second one differing by the white, scaly vestiture apressed to surface, laterally rounded abdomen, straight-sided pronotum, and rounded clypeus.

The food plant, *Guarea glabra* Vahl (Meliaceae) is a deciduous tree, with height of 3–15 m, ranged from Mexico to Colombia, Venezuela and Ecuador. In the region of “Los Tuxtlas,” Veracruz, Mexico, it is a dominant species within the forest (Ibarra-Manriquez, 1985).

*Etymology.* The specific epithet refers to the conspicuous scale-like setae over all of the body.

The key to species and species-groups of *Diplotaxis* in Vaurie (1960:188) should be modified as follows to incorporate *D. squamisetis*.

- |        |   |                    |
|--------|---|--------------------|
| 87(86) | Clypeus rounded from side to side as a semicircle, its front margin not reflexed;<br>Arizona; Chihuahua .....   | <i>mus</i>         |
| 87'    | Clypeus trapezoid, quadrate or rectangular in shape, angulate at sides, front margin reflexed; central, southern and eastern Mexico .....   | 87a                |
| 87a    | Dorsal vestiture formed by yellow scale-like setae, most of which are semierect;<br>clypeus rectangular with the front angles rounded, its frontal margin slightly reflexed; labrum twice longer than the reflexed under side of clypeus; Veracruz ...<br>.....             | <i>squamisetis</i> |
| 87a'   | Dorsal vestiture formed by white, depressed scales; clypeus trapezoid or quadrate<br>with the front angles obtuse or straight, its front margin strongly reflexed; labrum<br>of the same length or shorter than under side of clypeus; central and southern<br>Mexico ..... | 88                 |

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**STUDIES OF NEOTROPICAL CADDISFLIES, XLVII;  
KUMANSKIELLA, A NEW GENUS OF  
MICROCADDISFLIES FROM CUBA AND PUERTO RICO**

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*Abstract.*—A new genus of Neotrichiini, *Kumanskiella*, and new species *K. karenae*, from the Greater Antilles are described and illustrated. *Mayatrichia aliena* is transferred into this new genus. Keys to the genera of Neotrichiini are provided and a proposed phylogeny of the tribe presented. *Kumanskiella* appears most closely related to *Neotrichia* with *Taxatrichia* the sister group to *Mayatrichia*, *Kumanskiella* and *Neotrichia*.

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In 1987, Kumanski described *Mayatrichia aliena* from a single male collected from Sierra de Trinidad, Cuba. He placed the species in the genus *Mayatrichia* primarily on the basis of the four tibial spurs on the hindleg, but mentioned that in most characters of the male genitalia the species was similar to *Neotrichia*. Kumanski concluded that the species might be better placed in a new generic taxon, but with only a single specimen he left the taxonomic position unresolved.

In 1989, a series of microcaddisflies similar to *M. aliena* were collected from a malaise trap over a small stream in Puerto Rico by E. C. Masteller. A comparison of this material with the type of *M. aliena* revealed the specimens to represent a new, but closely related species. Larvae of this species were collected by Karen Buzby and were found, as with the adults, to possess characteristics intermediate between the genera *Mayatrichia* and *Neotrichia*. With both species fitting poorly within the generic limits of either *Mayatrichia* or *Neotrichia*, we herein erect the new genus *Kumanskiella*.

Morphological terminology used in the species descriptions follows that of Marshall, 1979. Length is measured from the top of the head to the tip of the forewings and is given as a range with more than one specimen. Type material will be deposited in the National Museum of Natural History (Smithsonian Institution), Center for Energy and Environmental Research (Puerto Rico), and the University of Alabama. The type of *Mayatrichia aliena* is deposited in the National Natural History Museum, Sofia, Bulgaria.

***Kumanskiella*, new genus**

Type species: *Kumanskiella karenae*, new species

*Adult.*—Head light brown in color, yellow between posterior warts; 3 ocelli; tentorium with anterior arms complete; antennae light brown, 18-segmented, about  $\frac{1}{3}$  length of forewing. Thorax light brown; pronotum narrow with pair of mesal and

lateral warts; mesoscutellum without transverse suture; metascutellum pentagonal. Forewings narrow, brown with no discernible pattern in alcohol, small lobe on posterobasal margin; hindwings brown, attenuate, patch of long setae on anterobasal margin. Legs yellow, tibial spur formula 0, 2, 4, outer spurs barely  $\frac{1}{2}$  length of inner spurs. Body circular in cross-section. Abdomen yellow; segment VI with short apicomosal projection.

*Male genitalia*.—Abdominal segment IX elongate posteroventrally in lateral aspect, bearing spine or sclerotized projection. Bracteoles present as lightly sclerotized lobes or acute projections from lateral margins of segment IX. Segment X membranous and indistinct dorsally. Inferior appendages well developed and elongate. Subgenital plate prominent, narrowing to distal beak in lateral aspect, in ventral view rounded basolaterally with mesal protuberance distally. Phallus with long tubular basal portion, sinuate asymmetrical median area bearing spiral process, apical portion bulbous beyond spiral process then tapering to narrow apex.

*Female genitalia*.—Segment VIII with pair of elongate apodemes; thin tongue-like process arising anteroventrally, tapering and projecting posteriorly. Segment IX with pair of short apodemes. Segment X short, rounded apically bearing pair of papillae subapically. Bursa copulatrix simple, narrow and elongate anteriorly and posteriorly, median portion oblong with thin cuneiform mesal sclerite.

*Larva*.—Head unicolorous brown, narrowing anteriorly in dorsal view, coronal and frontoclypeal sutures distinct, elongate seta posterior to eye, labrum well developed and covering mandibles. Thoracic nota unicolorous brown with medial ecdysial line; short, stout setae along anterior and anterolateral margins, few scattered short setae on dorsal surface; pleural sclerites well developed on meso- and metathorax, reduced on prothorax; prothoracic legs short with widened coxa and femur, meso- and metathoracic legs slender and elongate. Abdomen nearly cylindrical with distinct intersegmental grooves, lateral fringe of short setae, elongate seta dorsally and ventrally; abdominal segments IX and X with dorsal sclerites each bearing numerous elongate setae; anal prolegs elongate, projecting from body, anal claw short and stout. Larval case constructed of sand grains, slightly compressed dorsoventrally, gently tapering posteriorly, anterior and posterior openings semicircular.

*Etymology*.—Named in recognition of Krassimir P. Kumanski, who first collected the genus in Cuba.

#### **Kumanskiella karenae, new species**

Figs. 1–4

*Male*.—Length 1.5–1.9 mm. Brown in alcohol, no discernible pattern on wings. Antennae 18-segmented. Sternum of abdominal segment VI with short apicomosal process. Segment VIII square. Segment IX in lateral view narrowing posteriorly to a mesal, setose lobe, which bears a large distally-projecting spine; short rounded bracteoles arising mesally from inner surface; in ventral view deeply incised anteriorly, posteriorly broadly incised, each lateral arm bearing large spine; in dorsal aspect, broadly incised posteriorly and anteriorly, pair of oblong bracteoles originating near lateral margins and projecting distally. Segment X narrow in lateral view, membranous near apex; in dorsal aspect short and broadly rounded distally. Inferior appendages thin in lateral view, narrowing to rounded apex; in ventral view narrowly

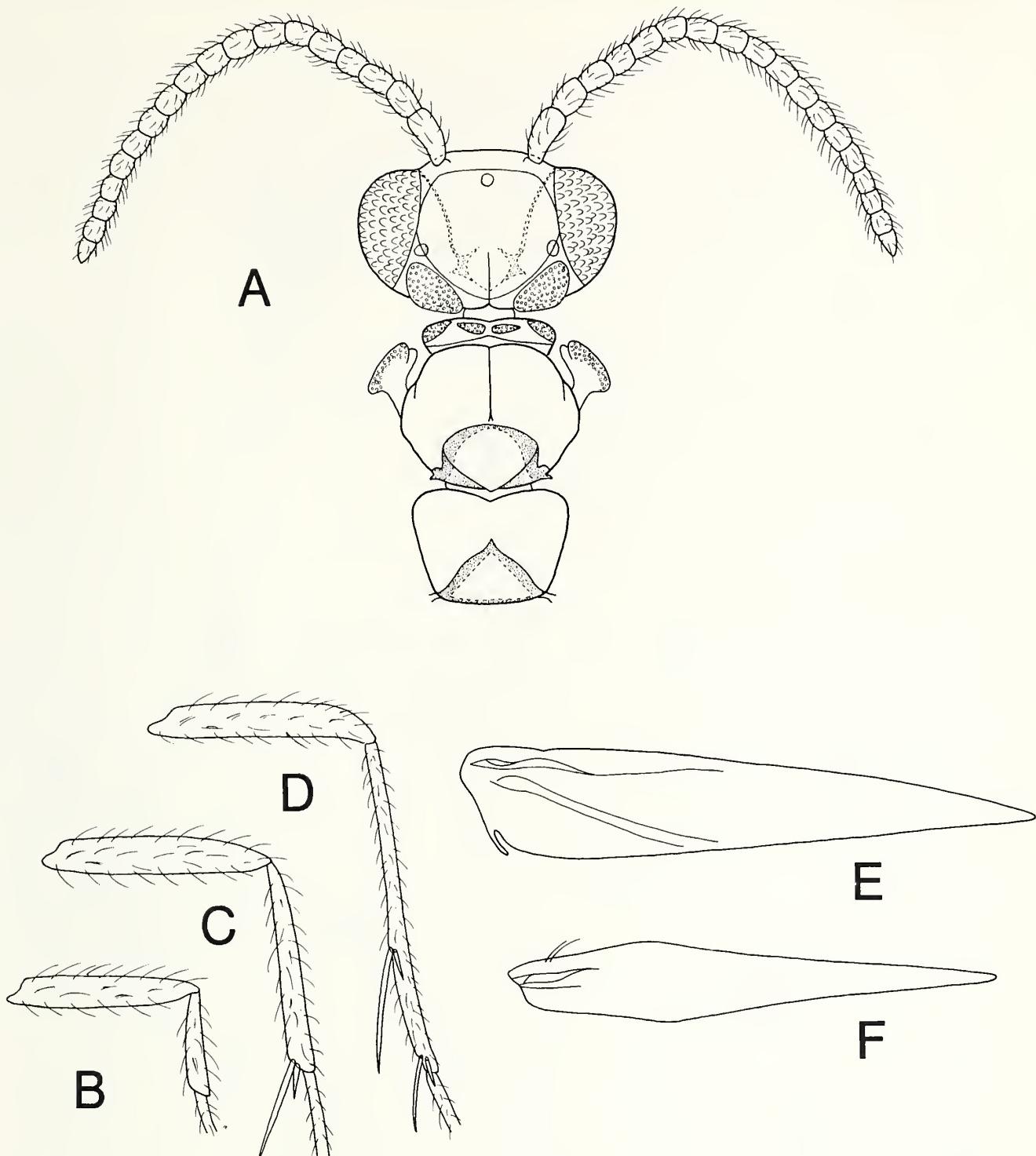


Fig. 1. *Kumanskiella karenae*, new species. Adult, male: A. Head and thorax, dorsal view. B. Prothoracic leg. C. Mesothoracic leg. D. Metathoracic leg. E. Forewing. F. Hindwing.

separated basally and tapering distally from broad base, slightly diverging at mid-length. Subgenital plate narrow, generally rectangular in lateral view; in ventral and dorsal aspects wide basally, with setae bearing knobs on inner margin, rounded laterally, narrowing to rounded apex, bearing pair of setae. Phallus with long, tubular basal portion, sinuate asymmetrical median area bearing spiral process, apical portion bulbous beyond spiral process then tapering to narrow apex.

*Female*.—Length 1.5–2.0 mm. Brown in alcohol. Antennae 18-segmented. Abdominal segment VI with short apicomosal process on venter. Segment VII truncate. Segment VIII elongate and narrow, fringe of setae on posterior margin, elongate

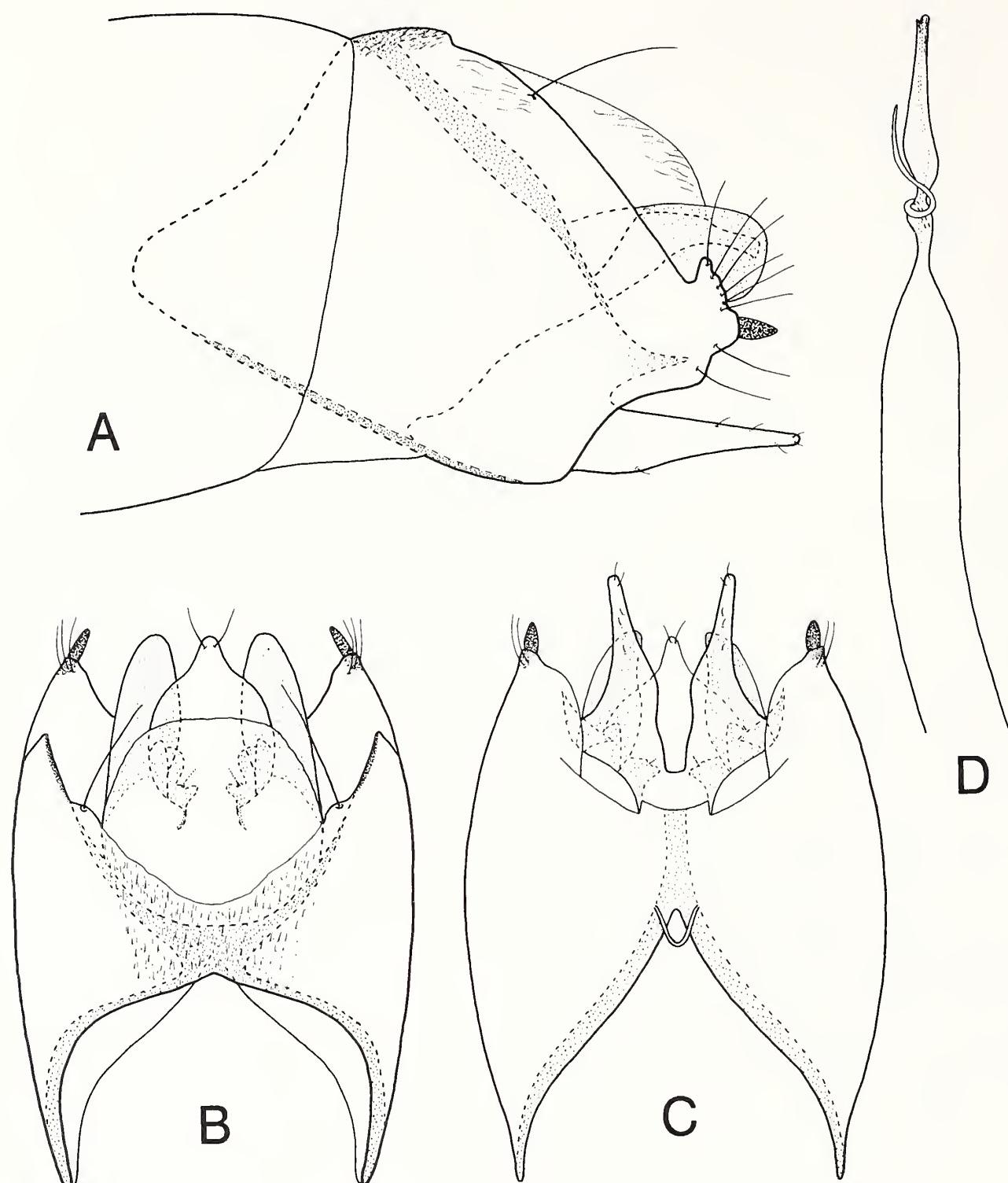


Fig. 2. *Kumanskiella karenae*, new species. Male genitalia: A. Lateral view. B. Dorsal view. C. Ventral view. D. Phallus, dorsal view.

tongue-like process arising anteroventrally, narrowing distally, pair of thin apodemes extending from lateral margins at juncture with segment VII and extending just into segment VI. Segment IX short, pair of median apodemes originating anterolaterally and extending anteriorly through segment VI. Segment X narrow and tapering to rounded apex, bearing pair of papillae subapically. Bursa copulatrix simple, narrow and elongate anteriorly and posteriorly, anterior extension about half length of posterior, median portion oblong with a thin mesal sclerite which is deeply incised anteriorly, smaller anterior sclerite with posterior notch.

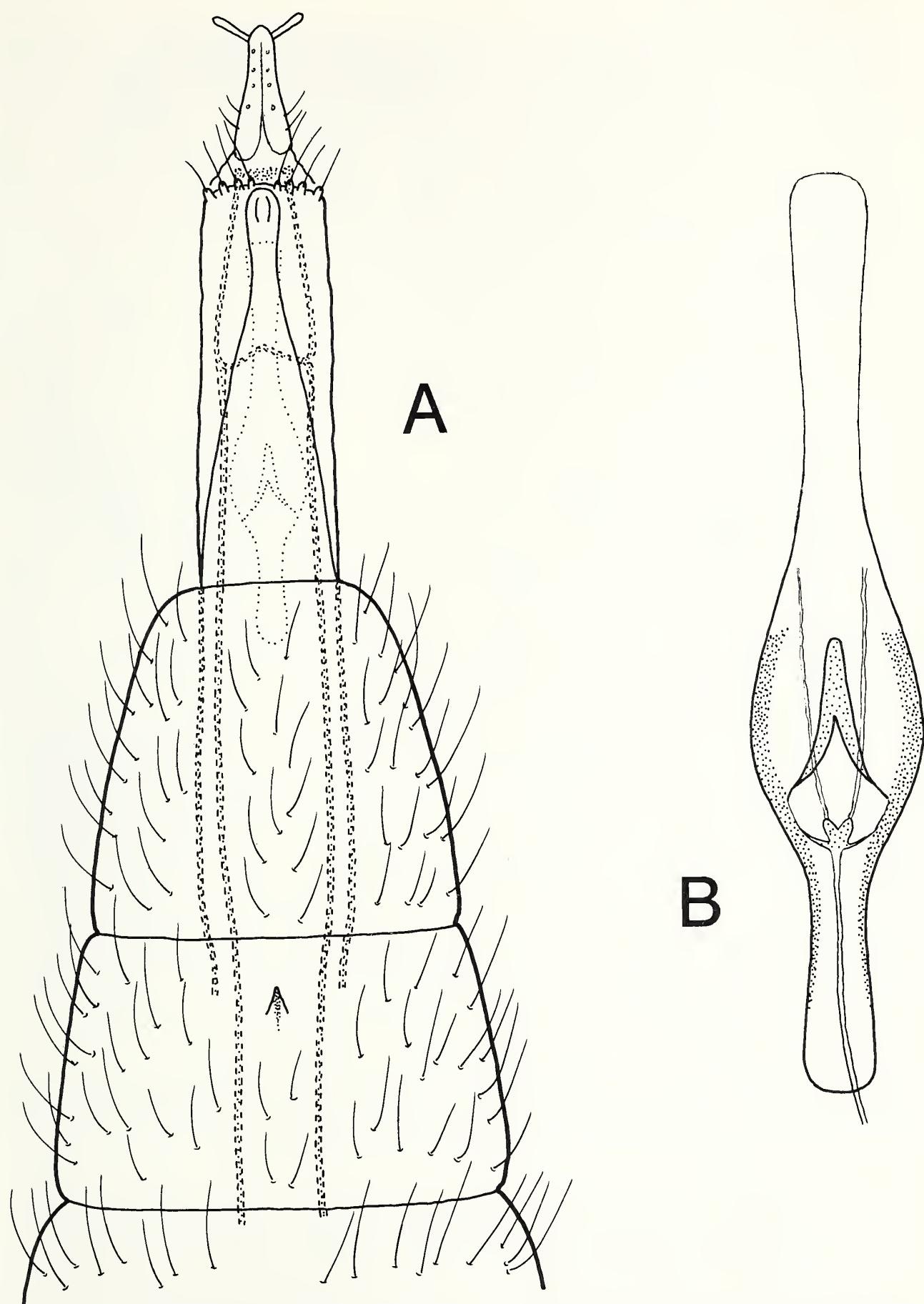


Fig. 3. *Kumanskiella karenae*, new species. Female genitalia: A. Terminal abdominal segments, ventral view. B. Bursa copulatrix, ventral view.

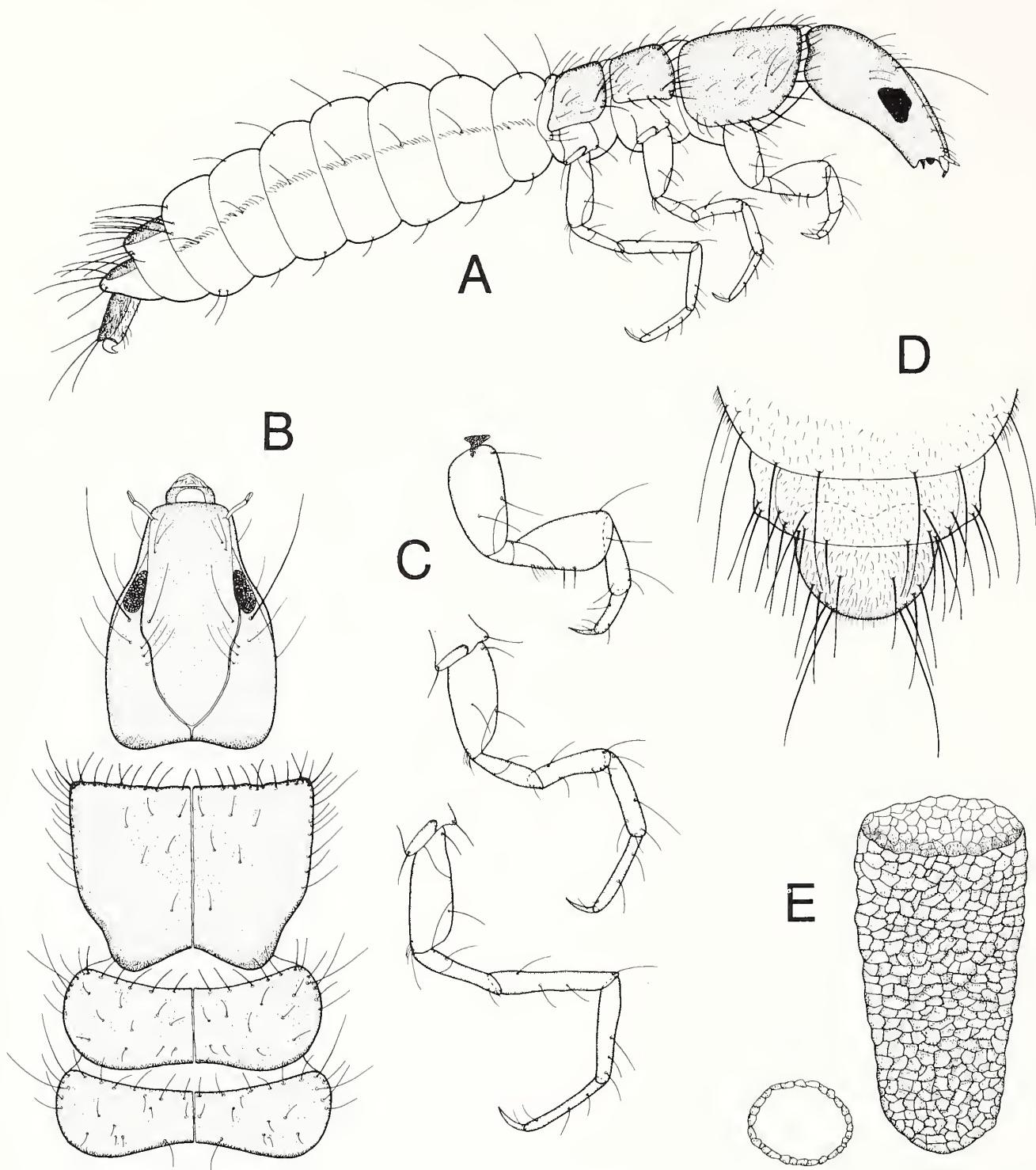


Fig. 4. *Kumanskiella karenae*, new species. Larva: A. Lateral view. B. Head and thorax, dorsal view. C. Pro-, meso-, and metathoracic legs, lateral view. D. Abdominal segments IX and X, dorsal view. E. Case, dorsal view, insert of posterior opening.

**Larva.**—Length 0.8–1.2 mm (10 larvae measured). Head unicolorous brown, slightly darker at posterior margin, narrowing anteriorly in dorsal view, coronal and frontoclypeal sutures distinct, the latter less so in anterior portion, numerous setae along frontoclypeal suture, elongate seta posterior to eye; antennae short, 2-segmented with second segment about  $\frac{1}{3}$  length of first; labrum well developed and elongate, covering mandibles. Thoracic nota heavily sclerotized, unicolorous brown, slightly darker at posterior margins, each notum with median ecdysial line; pronotum enlarged, about as wide as long, narrowing posterolaterally, setae along anterior and anterolateral

margins, seta short and stout, few scattered short setae near ecdysial line; meso- and metanota similar in shape, wider than long, short setae along anterior and antero-lateral margins and scattered over the dorsal surface; pleural sclerites well developed on meso- and metathorax, reduced to a small triangle on prothorax; prothoracic legs short with widened coxa and femur; meso- and metathoracic legs slender and elongate. Abdomen nearly cylindrical, with intersegmental grooves well defined, lateral fringe of short setae, elongate seta dorsally and ventrally, segments IX and X with dorsal sclerites each bearing numerous elongate setae; anal prolegs elongate, projecting from body, lateral sclerite of proleg elongate, bearing several setae posteriorly, anal claw short and stout. Larval case constructed of sand grains, slightly compressed dorsoventrally, and gently tapering posteriorly, anterior and posterior openings semi-circular. Length of case 0.9–1.6 mm (10 cases measured).

**Etymology.**—Named in recognition of Karen Buzby who has faithfully removed insects from the malaise trap and who collected and first recognized the larvae in her field samples.

**Type material.**—Holotype ♂. Puerto Rico, El Verde Field Station, Quebrada Prieta, malaise trap, 370 m, 6–10 February 1990, O.S. Flint, Jr.

**Paratypes.** Puerto Rico, same data as holotype, 13♂, 32♀; same locality, but all following from emergence trap; 22–27 February 1989, E.C. Masteller, 1♂, 3♀; March–May 1989, K. Buzby and E.C. Masteller, 1♂, 1♀; 20 February 1990, 1♀; 19 June 1990, 1♀; 25 June 1990, 1♂; 4 July 1990, 1♀; 7 July 1990, 1♀; 25 July 1990, 2♀; 8 August 1990, 1♂; 13 October 1990, 1♀; 10 December 1990, 2♂; 11 February 1991, 1♀; 13 February 1991, 1♂; 20 February 1991, 1♂, 1♀; 22 February 1991, 2♂, 2♀; 4 March 1991, 1♀; 6 March 1991, 1♀; 11 March 1991, 1♂, 2♀; 19 March 1991, 1♂, 2♀; 23 March 1991, 1♀; 27 March 1991, 1♂; 30 March 1991, 1♂; 5 April 1991, 1♂; 8 April 1991, 2♀; 17 April 1991, 2♂; 20 May 1991, 2♂; 19 June 1991, 1♂; 9 July 1991, 1♀; 13 July 1991, 1♂; 17 July 1991, 2♂; 29 July 1991, 1♂, 1♀. Puerto Rico, El Verde Field Station, Quebrada Toronja, bottom sample, 11 August 1990, K. Buzby, 2 larvae; 31 August 1990, 4 larvae; 11 October 1990, 1 larvae; 22 October 1990, 2 larvae; 12 December 1990, 4 larvae; 16 January 1991, 2 larvae.

**Habitat.**—Quebrada Prieta is a second order, high gradient mountain stream, averaging 20% slope, near El Verde in the Luquillo Experimental Forest of north-eastern Puerto Rico. The stream originates at approximately 600 meters above sea level (masl) and flows into the Quebrada Sonadora at 310 masl; the emergence trap was placed at 390 masl. The predominant substrates are bedrock, large boulders and cobble. The larvae were taken in the Quebrada Toronja, a very similar stream that is adjacent to the Prieta. These streams are all tributaries of the Rio Espiritu Santo. They flow through tabonuco forest, the predominant type on the Luquillo Mountains below 600 masl (preceding data supplied by K. Buzby, pers. comm.).

***Kumanskiella aliena* (Kumanski), New Combination**

Fig. 5

*Mayatrichia aliena* Kumanski, 1987:24.

**Male.**—Length 1.7 mm. Brown in alcohol. Antennae broken, but with at least 18 segments. Sternum of abdominal segment VI with short apicomosal process. Segment VIII square. Segment IX in lateral view narrowing posteriorly to form setose lobe,

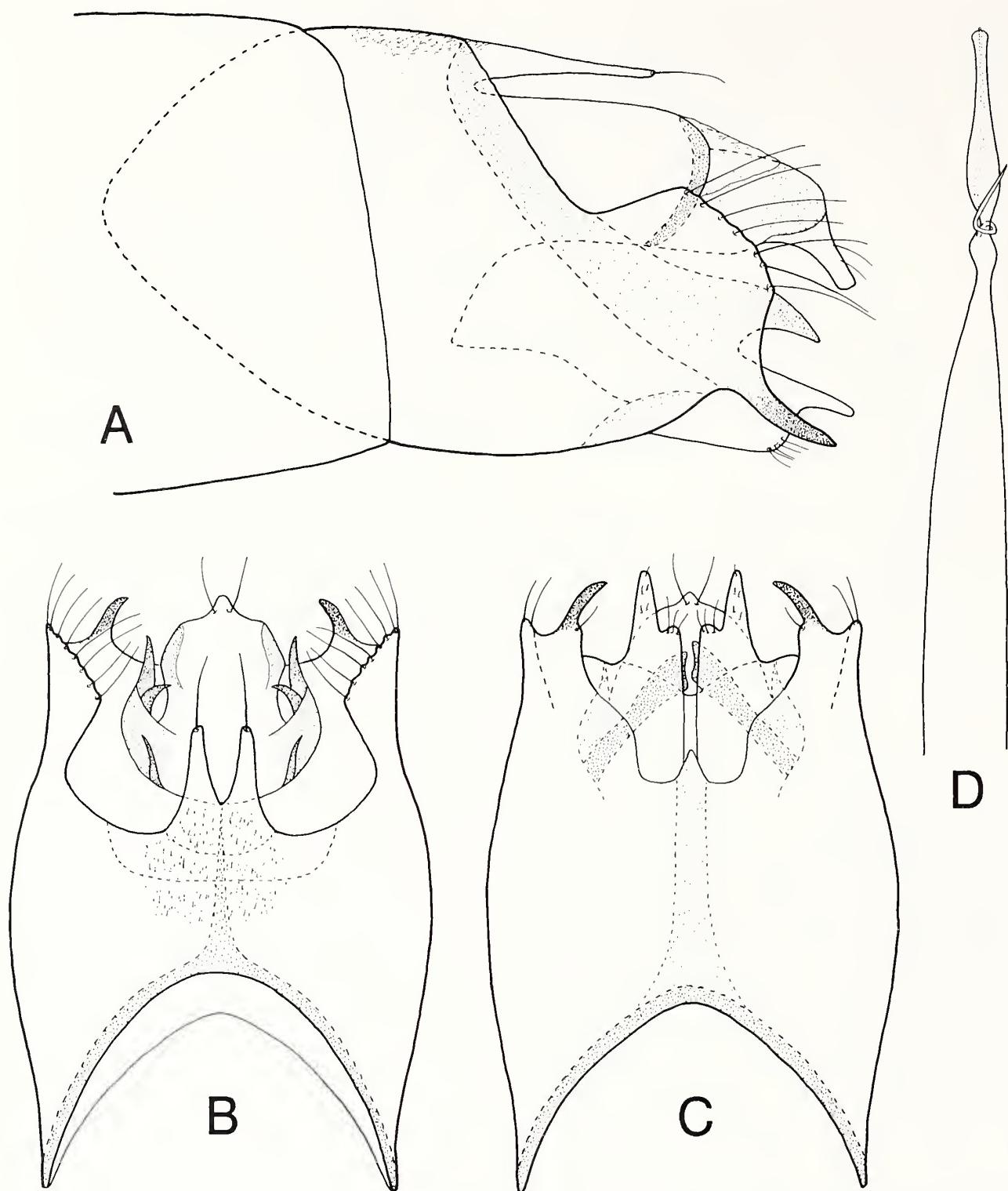


Fig. 5. *Kumanskiella aliena*, new combination. Male genitalia: A. Lateral view. B. Dorsal view. C. Ventral view. D. Phallus, dorsal view.

posteroventral margin with elongate, acute process; dorsally with pair of long, finger-like processes mesally, each bearing long seta apically; incised mesally in ventral view, each lateral arm with heavy sclerotized spine directed inward; bracteoles sclerotized and originating on inner posterolateral margins, in lateral view falciform, in ventral view elongate and narrow, slightly emarginate apically. Segment X membranous and indistinct dorsally, ventrolateral margins developed as an obliquely curved sclerite, in dorsal aspect visible as acute lateral projections, directed posteriorly. Inferior appendages in lateral view rectangular with elongate dorsal extension

distally; in ventral view narrowly separated along straight inner margins, lateral digitiform extension distally. Subgenital plate in lateral view with prominent distal beak projecting somewhat ventrad; in dorsal view narrow with sinuate lateral margins, distally with mesal protuberance bearing pair of subapical setae. Phallus with long, tubular basal portion, sinuate asymmetrical median area bearing spiral process, apical portion slightly bulbous beyond spiral process then tapering to thin, slightly flared apex.

*Female*.—Unknown.

*Larva*.—Unknown.

*Type locality*.—Cuba: Province Las Villas, Sierra de Trinidad, small torrent on the road Trinidad-Topes de Collantes, 150 m, 3 December 1982.

#### SYSTEMATIC RELATIONSHIPS

The Neotrichiini as presently defined (Marshall, 1979) are restricted in distribution to the New World with species occurring throughout North, Central, and South America, including the West Indies. The tribe is now comprised of four genera, *Taraxitrichia*, with a single species from Venezuela (Flint and Harris, 1991), *Kumanskiella*, with two species from the Greater Antilles, *Mayatrichia* with five species from North, Central and northern South America (Harris and Holzenthal, 1990) and *Neotrichia* with over 80 species and a widespread distribution over the Americas. These genera are readily distinguished as adults and larvae, as far as they are known (the immature stages of *Taraxitrichia* are as yet unknown) (Table 1).

#### KEY TO ADULT MALE NEOTRICHIIINI

1. Mesothoracic leg with three tibial spurs; without ocelli ..... *Taraxitrichia*
- Mesothoracic leg with two tibial spurs; with ocelli ..... 2
- 2(1). Metathoracic leg with three tibial spurs ..... *Neotrichia*
- Metathoracic leg with four tibial spurs ..... 3
- 3(2). Bracteoles elongate (Harris and Holzenthal, 1990, fig. 1A); phallus tubular and lacking spiral process (Harris and Holzenthal, 1990, fig. 1D) ..... *Mayatrichia*
- Bracteoles not clearly evident (Fig. 2A); phallus with spiral process and divided into basal and distal portions (Fig. 2D) ..... *Kumanskiella*

#### TENTATIVE KEY TO LARVAE<sup>1</sup>

1. Thoracic nota with elongate hairs along the margins and scattered on the surface (Wiggins, 1977, fig. 7.8F) ..... *Neotrichia*
- Thoracic nota with short, stout setae along the margins and scattered on the surface (Fig. 4A, B; Wiggins, 1977, fig. 7.7F) ..... 2
- 2(1). Larval case constructed of sand grains (Fig. 4E); abdominal segments well defined (Fig. 4A) ..... *Kumanskiella*
- Larval case constructed of silk, walls reinforced with ridges (Wiggins, 1977, fig. 7.7B; Ross 1944, fig. 558); abdominal segments poorly defined (Wiggins, 1977, fig. 7.7A) ..... *Mayatrichia*

<sup>1</sup> The key is tentative since only a few species of Neotrichiini have associated larval stages and the larva of *Taraxitrichia* is unknown. Since *Taraxitrichia* appears to be closely related to *Mayatrichia*, we would expect the larvae to be similar in overall appearance.

Table 1. Characteristics of the Neotrichiini.

	Adult					Larvae		
	Tibial spurs	Ocelli	Bracteoles	Phallus	Bursa copulatrix	Case	Thoracic setae	Abdominal segments
<i>Neotrichia</i>	0,2,3	3	Often present	Complex	Thin cuneiform vaginal sclerite	Sand	Elongate	Distinct
<i>Kumanskiella</i>	0,2,4	3	Poorly defined	Complex	Thin cuneiform vaginal sclerite	Sand	Short	Distinct
<i>Mayatrichia</i>	0,2,4	3	Present	Simple	Vaginal sclerite with anterior lobes	Silk	Short	Indistinct
<i>Taraxitrichia</i>	0,3,4	0	Present	Simple	Vaginal sclerite with anterior lobes	—	—	—

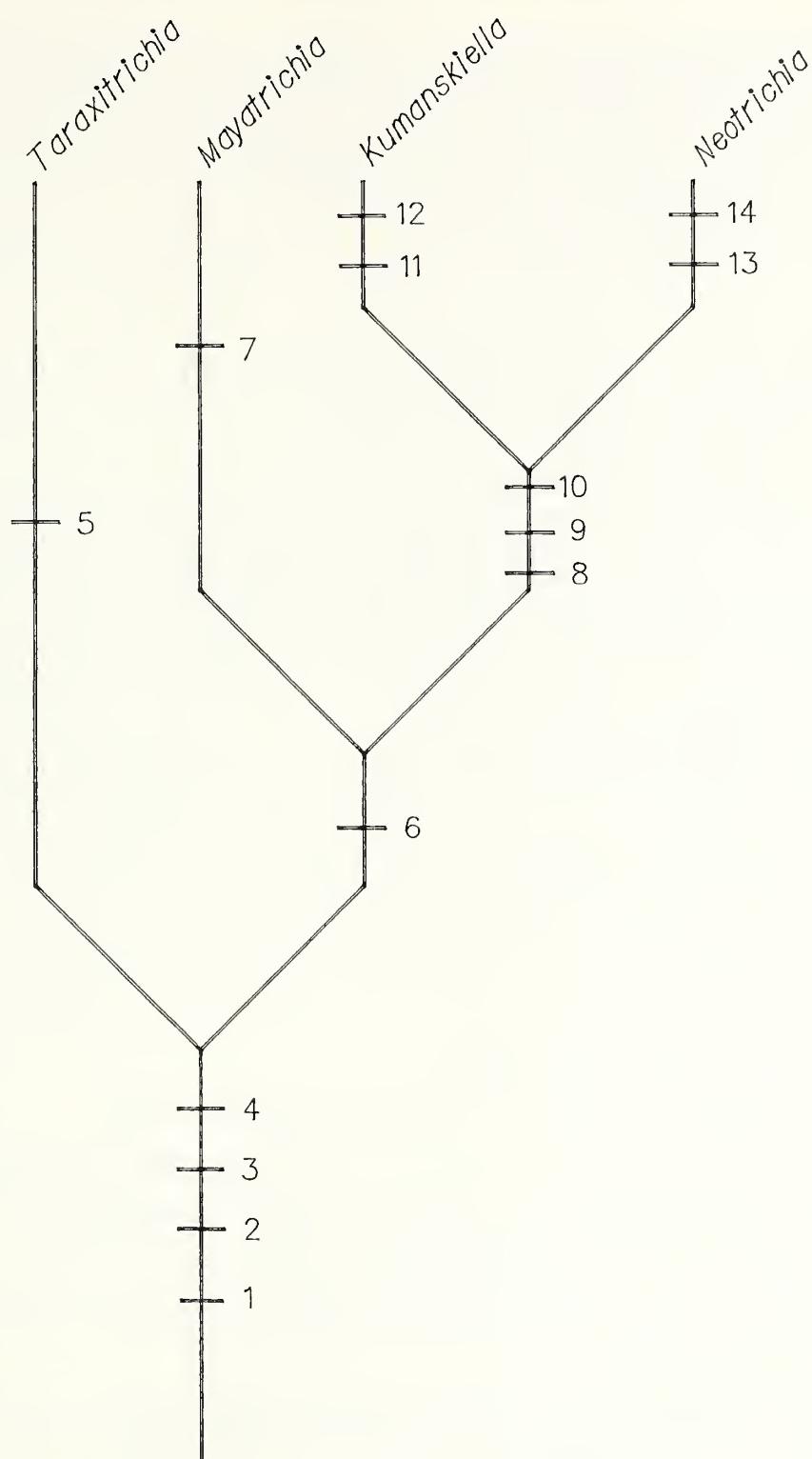


Fig. 6. Proposed phylogeny of the genera of Neotrichiini.

Although Marshall (1979) summarized much of the current knowledge of the Hydroptilidae, she only suggested phylogenetic placement of the tribes, giving neither characters nor producing a cladistic analysis. In her Chart II, Marshall places the Ochrotrichiini as the basal sister group to a clade inclusive of the Neotrichiini, Hydroptilini, Orthotrichiini, and several unplaced genera. The Ochrotrichiini are characterized by having a tibial spur formula of 1, 3, 4 or 0, 3, 4, simple phallus without spiral process, 3 ocelli, and a transverse suture on the mesoscutellum.

The Ochrotrichiini are here considered the out-group to the Neotrichiini in order

to root the proposed phylogeny of Figure 6. Monophyly of the Neotrichiini is supported by the following synapomorphies:

1. Bracteoles originating from posterior margin of abdominal segment IX;
2. Lack of a transverse suture on the mesoscutellum;
3. Larvae constructing cylindrical cases;
4. Anal prolegs of larvae, elongate, cylindrical and projecting prominently.

*Taraxitrichia* appears to be the sister group to the other genera in the tribe as it retains the plesiomorphic condition of the third tibial spur on the mesothoracic leg and the simple phallus which lacks a spiral process. However, the absence of ocelli (5) in this genus is autapomorphic.

*Mayatrichia*, *Kumanskiella* and *Neotrichia* share the apomorphic condition of the mesothoracic leg having two tibial spurs (6). *Mayatrichia* is distinguished on the basis of the larvae having poorly defined abdominal segments (7). *Mayatrichia* retains the simple phallic structure which is plesiomorphic. With *Taraxitrichia*, *Mayatrichia* shares the character of the females having a bursa copulatrix with a pair of anterior lobes (Harris and Holzenthal, 1990, fig. 2B). As well, both these genera have several species with an elongate sternal process on the abdomen of the males. If we consider these to be plesiomorphic characters possessed by the hypothetical ancestor of the tribe (HTU), then a shortening of the sternal process, a character reversal, seen in both *Kumanskiella* and *Neotrichia*, as well as a loss of the anterior lobes of the bursa copulatrix seen in these two genera is apomorphic.

Monophyly for *Kumanskiella* and *Neotrichia* is inferred by three synapomorphies:

8. Complex phallic structure, usually with distinct distal and basal sections and spiral process;
9. Larvae with cylindrical sand cases;
10. Bursa copulatrix with narrow, cuneiform vaginal sclerite.

Both genera also have in common, larvae with well defined abdominal segments which is probably plesiomorphic since larvae of Ochrotrichiini also have this character. However, another possibility is that the HTU had larvae with poorly defined abdominal segments, with a reversal of the character state in *Kumanskiella* and *Neotrichia*. The interpretation of this larval character will be clearer with the discovery of the larvae of *Taraxitrichia*.

*Kumanskiella* is distinguished by the modified bracteoles (11) which are difficult to discern, and the asymmetrical median portion of the phallus (12). *Neotrichia* is distinctive in that the metathoracic leg has only three tibial spurs (13) and the larvae have elongate setae on the thoracic nota (14).

#### ACKNOWLEDGMENTS

Dr. Krassimir Kumanski, Director, National Natural History Museum, Sofia, Bulgaria, kindly lent the type of *Mayatrichia aliena* for comparison as well as several *Neotrichia* from Cuba and was very helpful in our diagnosis of the new genus. Dr. E. C. Masteller, Behrend College, Pennsylvania State University, Erie, Pennsylvania, first installed the emergence traps on Quebrada Prieta and has continued to oversee this operation and has sent all the caddisflies to OSF for identification. Karen Buzby, College of Environmental Science and Forestry, State University of New York, Syracuse, New York, has emptied these traps several times a week over the last

two years, and recognized the larvae of *Kumanskiella* in the bottom samples taken for her thesis work. The research of Masteller and Buzby on the Quebrada Prieta was supported by grant BSR-8811902 from the National Science Foundation to the Center for Energy and Environment Research (University of Puerto Rico) and the Institute of Tropical Forestry (Southern Forest Experiment Station) as part of the Long-Term, Ecological Research Program in the Luquillo Experimental Forest. R. L. Mayden, University of Alabama, was very helpful in the phylogenetic analysis and construction of Figure 6.

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FIRST INSTAR DESCRIPTION OF *KORSCHELTELLUS GRACILIS* (GROTE) AND *STHENOPIS AURATUS* (GROTE) (LEPIDOPTERA: HEPIALIDAE) WITH A CONSIDERATION OF CLADISTIC RELATIONSHIPS BETWEEN SETAE

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*Abstract.*—The external morphology and chaetotaxy of first instar *Korscheltellus gracilis* (Grote) and *Sthenopis auratus* (Grote) are described. The larvae of *K. gracilis* are smaller and have fewer microtrichia than *S. auratus*. The only difference in chaetotaxy involves the absence of pore Va from the head of *S. auratus*. The setal nomenclatures of Hasenfuss (1969) and Wagner (1987) are evaluated and used for description. The classifications of Hinton (1946) and Hasenfuss (1969) are compared for the homology of cranial setal groups. In a comparison of the P and V setae we suggest that homologies are treated as apomorphies by Hasenfuss, while Hinton's setal homologies represent plesiomorphies. Hasenfuss's (1969) nomenclature renders the cranial chaetotaxy of Hepialidae identical to the Ditrysia. We suggest that the prothoracic association of SD1, SD2 and D2 may represent an exoporian apomorphy. Cladistic criteria provide a useful technique for resolving homology problems and choosing between alternative systems of chaetotaxy.

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*Korscheltellus gracilis* (Grote) is a common eastern North American insect of upper elevation boreal forest soils (Wagner, 1988; Tobi et al., 1989; Wagner et al., 1989; Leonard et al., 1991; Wagner et al., 1991; Grehan et al., 1992; Tobi et al., 1992). Larvae feed on mosses, ferns and tree roots, including roots of red spruce (*Picea rubens* Sargent) and balsam fir (*Abies balsamea* (L.) Miller), which are species of major concern for environmental scientists interested in boreal forest dynamics and tree decline (e.g., Reiners and Lang, 1979; Siccamo et al., 1982; Hornbeck and Smith, 1985; Hain, 1987; Klein and Perkins, 1988; Vogelmann et al., 1988; Bonan and Shugart, 1989; Pitelka and Raynal, 1989; Silver et al., 1991; Smith, 1991).

Larvae of *Sthenopis auratus* (Grote) feed on roots, stems and leaf bases of ostrich fern (*Matteuccia struthiopteris* (L.) Todaro) (McCabe and Wagner, 1989) and wood fern (*Dryopteris campyloptera* Clarkson) (JGL unpubl. data). They are infrequently recorded from the spruce-fir zone (1,000 m elev.) on Camels Hump Mt., Huntington, VT, but are common at 200 m in the University of Vermont Experimental Research Forest, Jericho, VT. At our Camels Hump field site one *S. auratus* and 1,200 *K. gracilis* larvae were recovered from 110 soil pits (Leonard et al., 1991).

The post-first instar chaetotaxy of *K. gracilis* was described by Wagner et al. (1989) using Stehr's (1987) modification of Hinton (1946). The post-first instar of *S. auratus* was described and the chaetotaxy discussed, but not illustrated, by McCabe and Wagner (1989). Hepialid larvae have been described by a number of authors (e.g., Dyar, 1895; Packard, 1895; Fracker, 1915; Forbes, 1923; Gerasimov, 1937, 1952; Hinton, 1946; Hasenfuss, 1963, 1969; Aitkenhead and Baker, 1964; Hardy, 1973;

Table 1. Hepialidae head chaetotaxy according to Hinton (1946), Hasenfuss (1963, 1969), Wagner (1987), and Wagner et al. (1989) (modified from Stehr, 1987). Setal names in parentheses, mislabeling in square brackets.

Hinton	Hasenfuss	Wagner
A1 (Anterior)	A3	A1
A2	A2	A2
A3	P2	A3
O1 (Ocellar)	A1	S1 (Stemmatal)
O2	O1	S2
SO1 (Subocellar)	SO1	SS1 (Sub-stemmatal)
SO2	SO2	SS2
SO3	SO3	SS3
F1 (Frontal)	F1	F1
Fa (pore)	Fa	Fa
C1 (Clypeal)	C1	C2
C2	C2	C1
L1 (Lateral)	L1	L1
La (pore)	La	La
P1 (Posterodorsal)	P1	P1
P2	V1 (Vertexal)	P2
V2	V2	MD2 [MD1]
V3	V3	MD3
Va (pore)	Va	MDa [MD2]
G1 (Genal)	G1	MG1 (Micro-genal)
G2	O3	MG2

Grehan, 1981; Grehan et al., 1983; Yasuda and Abe, 1986; Wagner, 1987; McCabe and Wagner, 1989; Nielsen and Kristensen, 1989; Wagner et al., 1989; Common, 1990; Boudinot, 1991). Nomenclatural systems for hepialid chaetotaxy and cranial pores proposed as modifications to Hinton (1946) include Hasenfuss (1969), Nielsen and Kristensen (1989), Yasuda and Abe (1986), Stehr (1987), and Wagner (1987). With the exception of Hasenfuss (1963, 1969), the alternatives are presented without extensive comparative corroboration.

The chaetotaxy of first instars is different from second and later instars and may be more conservative. First instars, therefore may contribute significant information about phylogenetic relationships within the Exoporia (Nielsen, 1989). However, out of an estimated 500 species in the Hepialidae (Kristensen, 1978), descriptions of first instar Hepialidae are limited to about 10 species (Dyar, 1895; Fracker, 1915; Hinton, 1946; Aitkenhead and Baker, 1964; Grehan, 1981; Grehan et al., 1983).

This description of *K. gracilis* and *S. auratus* first instars will refer to Hasenfuss's (1969) setal nomenclature for the head, Wagner's (1987) system for the prothorax (TI) (with the addition of the Hasenfuss [1963] notation for the XD pores which were not illustrated in Wagner [1987]), and Hinton (1946) for the meso- and metathorax (TII, TIII) and abdomen (A1–A10). We will discuss these nomenclatural systems in relation to our observations on the first instars and comparisons with Hepialidae described in the literature. Tables 1 and 2 compare the hepialid nomenclatural systems currently in use.

Table 2. Prothorax chaetotaxy used for Hepialidae according to Hinton (1946), Nielsen and Kristensen (1989), Wagner (1987), and Wagner et al. (1989).

Hinton	Nielsen and Kristensen	Wagner
D1 (Dorsal)	D1	D1
D2	D2	SD2 (Sub-dorsal)
XD1 (Extra-dorsal)	XD1	XD1
XD2	XD2	XD2
XDb (pore)	XDa	—
XDa	XDb	—
XDc	XDc	—
SD1	SD1	SD1
SD2	SD2	D2
L1 (Lateral)	L1	L1
L2	L2	L2
L3	L3	L3
SV1 (Sub-ventral)	SV1	SV1
SV2	SV2	SV2
MV2 (Mid-ventral)	MV2	MV2
MV3	MV3	MV3
V1 (Ventral)	V1	V1

We have confined our description to body setae and pores with the exclusion of the larval thoracic leg and abdominal proleg setae. Comparative chaetotaxy of thoracic and abdominal legs has received little attention but several alternative systems have been proposed (e.g., Gerasimov, 1952; Birket-Smith, 1984; Nielsen and Kristensen, 1989).

#### MATERIALS AND METHODS

*Korscheltellus gracilis* eggs were collected on 25 July 1990 from a female that was in copula on a balsam fir branch apex 1 m above ground at 1,000 m elevation on Camels Hump Mountain, Huntington, Vermont. The mating pair and fir branch were enclosed in a plastic bag after the evening flight (approximately 9 pm EST) and eggs recovered the following morning. *Sthenopis auratus* eggs were collected on 14 July 1990 from a female found in copula on the frond tip of ostrich fern at the University of Vermont Experimental Research Forest in Jericho, VT. Eggs were incubated on moist filter paper inside petri dishes in a saturated atmosphere at 18°C.

First instars were preserved in 70% EtOH. The head capsules of 8 *S. auratus* and 24 *K. gracilis* were measured to the nearest 0.001 mm. Means and 95% confidence intervals for head capsule measurements were computed using univariate descriptive procedures in SAS (1985). Sub-samples of larvae were randomly chosen for examination by scanning electron (SEM) and light microscopes. Light microscope slides were prepared as described in Aitkenhead and Baker (1964). In addition, some larvae were cleared with KOH and temporarily slide-mounted in glycerine. Descriptions presented refer to both species unless otherwise indicated.

## RESULTS

Eggs of *K. gracilis* hatched in 26 days and those of *S. auratus* hatched in 30 days. Eggs of *S. auratus* were larger than those of *K. gracilis*.

**Head.** The head capsule is straw-colored and large relative to the body size, especially for *K. gracilis*. The head capsule widths of *S. auratus* (mean = 0.546 mm, standard error  $\pm$  0.002 mm, N = 8) were significantly larger than that of *K. gracilis* (0.332 mm  $\pm$  0.002 mm, N = 24). Head setae of *S. auratus* were shorter relative to the head size than on *K. gracilis* and the shape of the head capsule, adfrontal suture, and mandible was different between species (Figs. 1–6).

The antenna appears 3-segmented, but may be 2-segmented as described for *Fraus* by Nielsen and Kristensen (1989). Antenna is shorter and thicker than in the post-first instar (cf. McCabe and Wagner, 1989; Wagner et al., 1989). Each antenna bears three conical sensilla and three trichoid sensilla with the lateral trichoid sensillum 1.5 times the length of the antenna. The anterior-most trichoid sensillum arises from the base of the most anterior conical sensillum (Figs. 7–8).

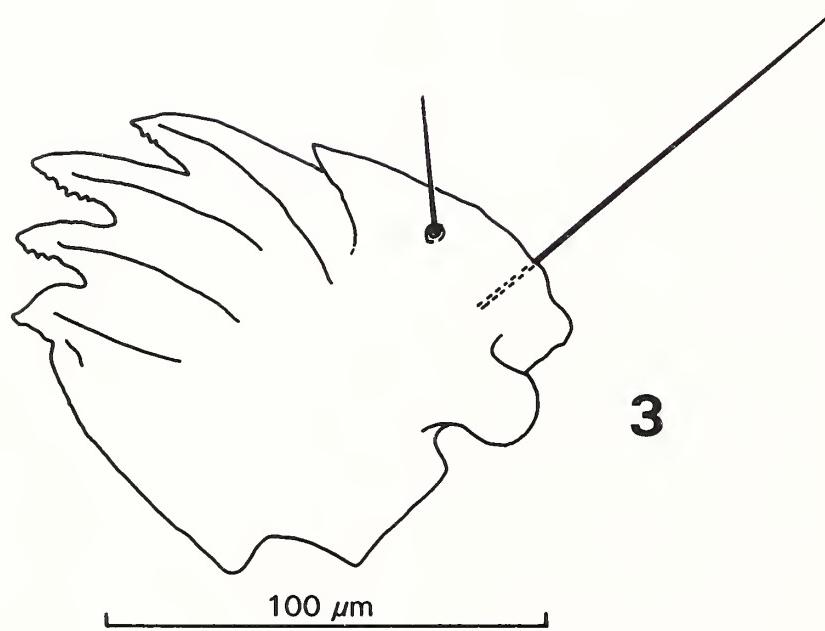
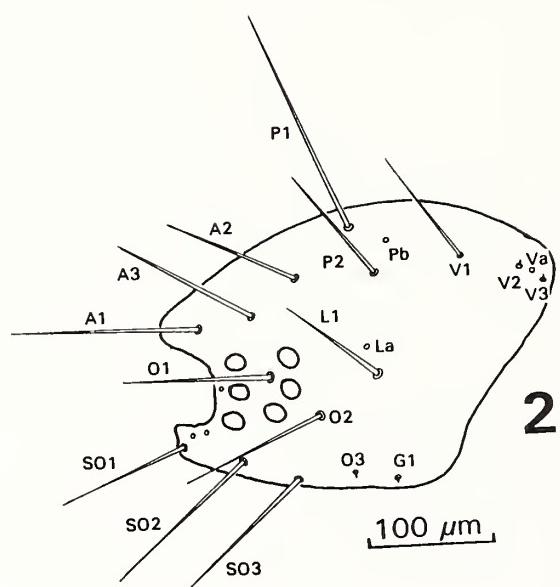
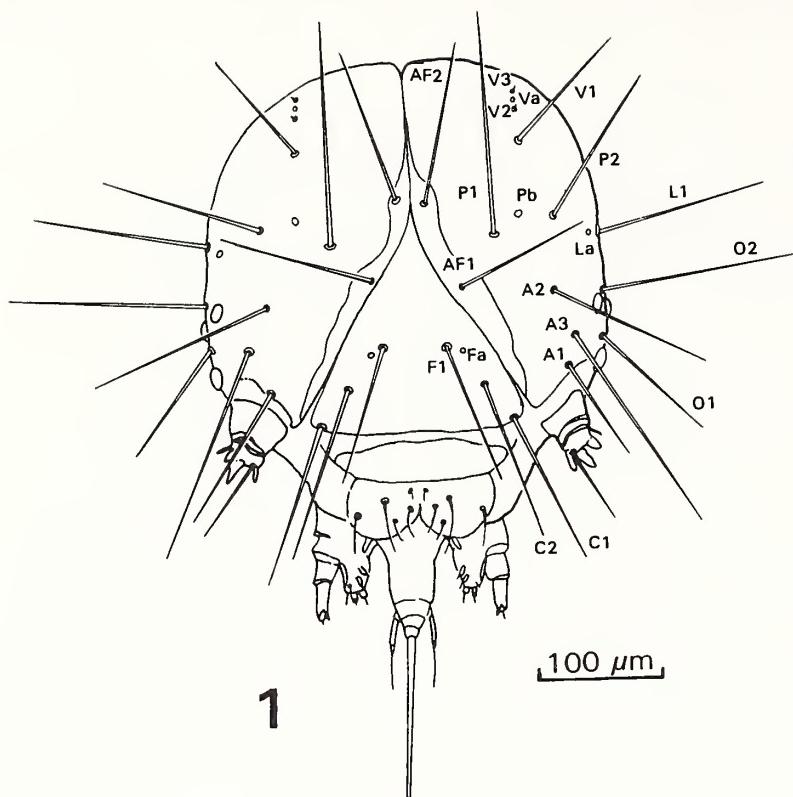
The labrum is deeply cleft with 5 pairs of setae. The mandible has 5 teeth. The middle three teeth are serrate on ventrad edge. The mandible has 2 setae; one small seta located on the dorsal tooth, the second 1.5 times the mandible length and inserted into the mandible base (Figs. 3, 6).

The maxillae of both species are as described for post-first instar *K. gracilis* (Wagner et al., 1989), except the palpi are thinner and more elongate (Figs. 9–13). Each maxilla bears a stout trichoid sensillum on the dististipes, a 3-segmented maxillary palpus, and a mesal lobe (lobarium) with 1 trichoid sensillum on the base and 7 sensilla on the apex. Unlike later instars, the basal trichoid sensillum on the mesal lobe is subequal in length to the lobe. The apical sensilla of the mesal lobe consists of 2 styloconic sensilla, 3 small trichoid sensilla, and 2 larger trichoid sensilla. The basal segment of the maxillary palpus bears a pore on the lateral side. The apical end of the palpus bears larger, more prominent sensilla than in later instars including at least 4 trichoid sensilla and 1 squamiform sensillum (Fig. 11–13). (The maxillary palpus of *K. gracilis* is incorrectly labeled the labial palpus in Wagner et al. [1989: 721, Fig. 11].)

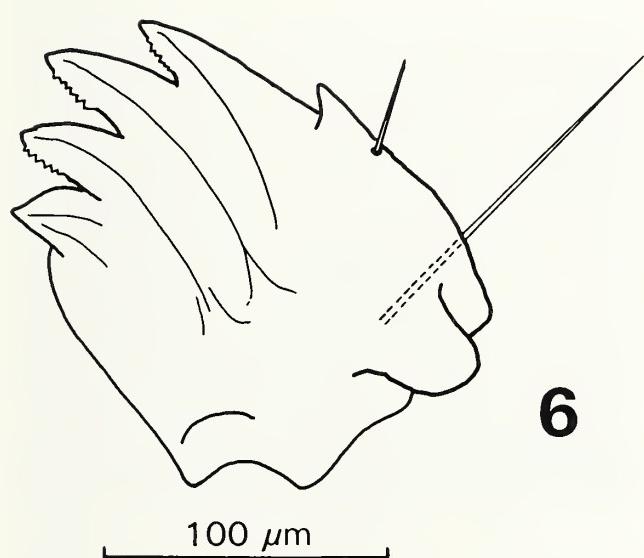
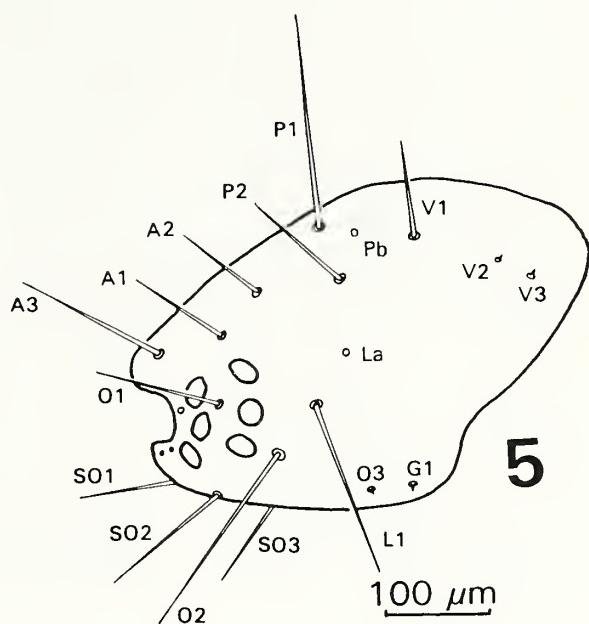
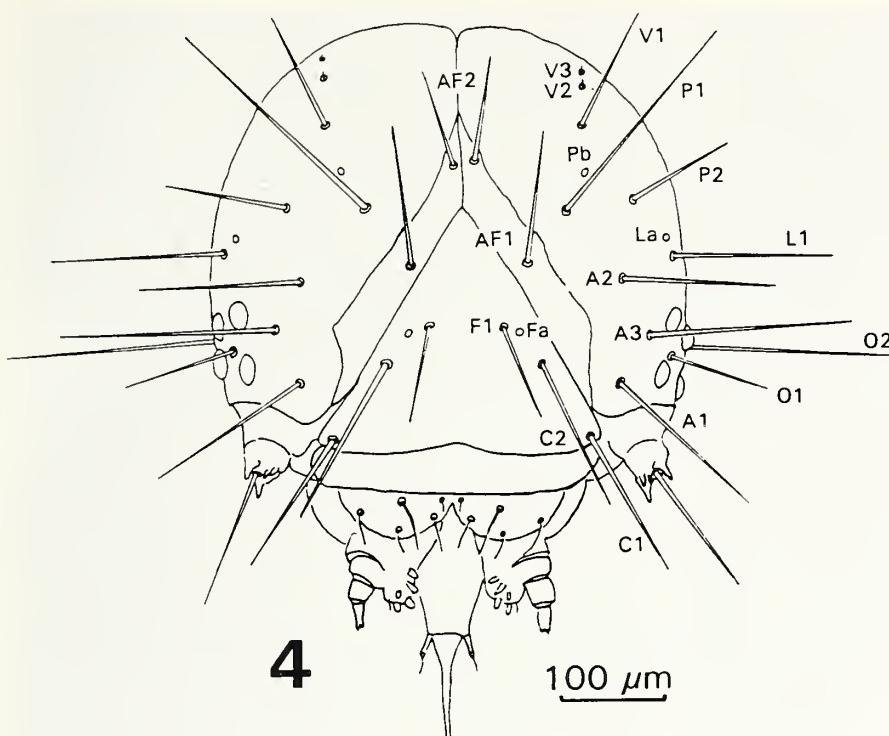
The hypopharynx and labium for both *K. gracilis* and *S. auratus* are nearly as described for post-first instars by Wagner et al. (1989). The labial palpus is 2-segmented, but the number is uncertain for the later instars (Wagner et al., 1989). The distal segment is short and conical, bearing a trichoid seta subequal in length to the palpus (Fig. 12). The spinneret of both species is approximately equal to the length of the maxillolabial-hypopharyngeal complex and is oriented ventro-caudad (Figs. 1, 4, 14–15). The hypostomal plates are not fused at the midline for both *K. gracilis* and *S. auratus* first instars.

In larvae of *K. gracilis* the pore **Va** (=MD2 of Wagner et al., 1989) is positioned between the two vertex (**V**) setae (N = 6) as in other Hepialidae (Figs. 1–2), but missing in *S. auratus* (N = 7) (Figs. 4–5, 16, 17). The pore **MDa** was misidentified as microseta **MD2** in Wagner et al. (1989), resulting in the anterior microseta **MD2** being misidentified as **MD1**. Setae **A1** and **S1** were also mislabelled (Wagner et al., 1989:721, fig. 8) as **A3** and **S3** respectively.

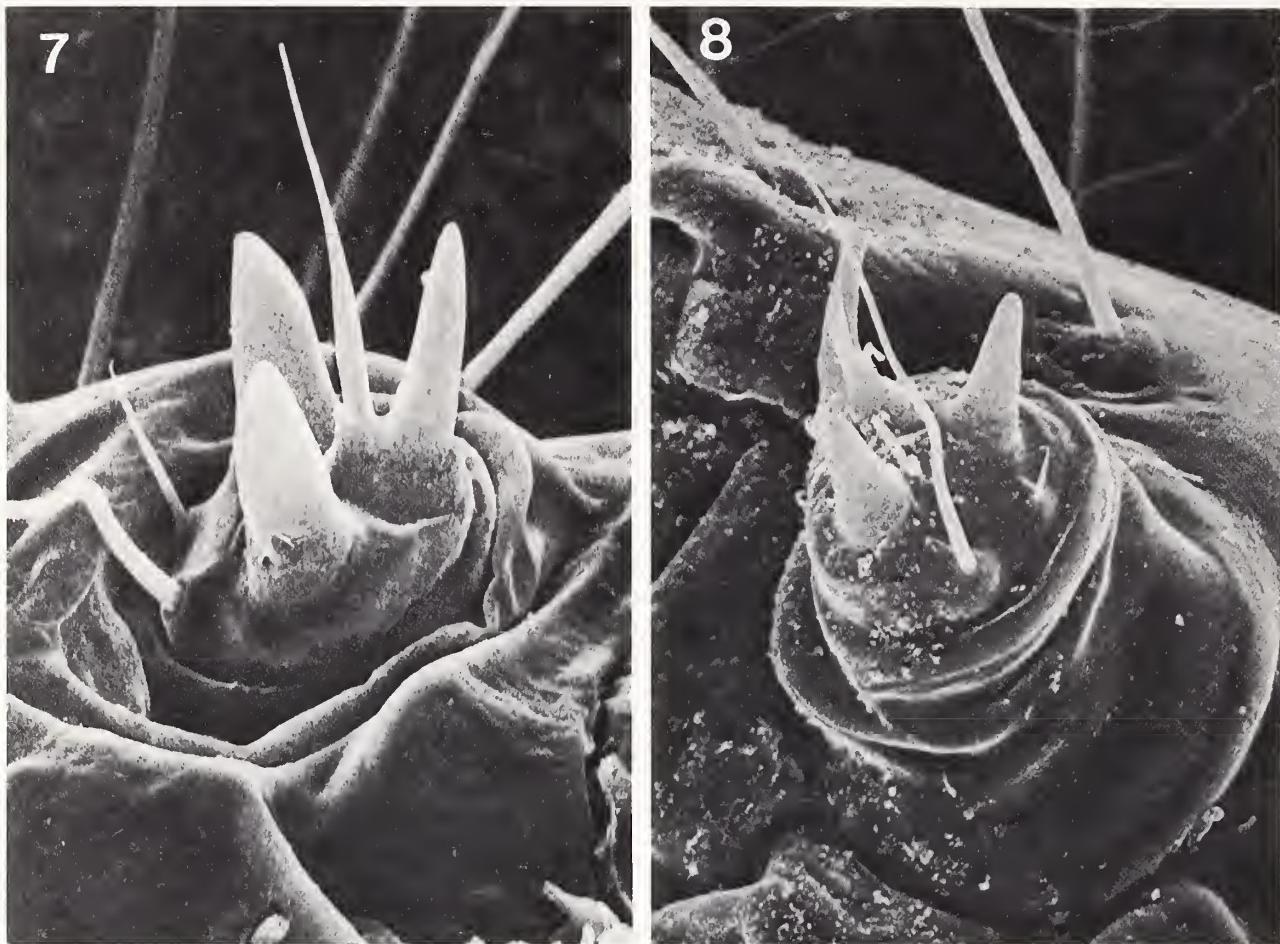
First instars of both *K. gracilis* and *S. auratus* show all of the setal characters present in later instars except for the lack of subprimary setae (see Tables 1 and 2



Figs. 1–3. *Korscheltellus gracilis* first instar head chaetotaxy. 1. Dorso-frontal view. 2. Lateral view. 3. Mandible.



Figs. 4–6. *Sthenopis auratus* first instar head chaetotaxy. 4. Dorso-frontal view. 5. Lateral view. 6. Mandible.

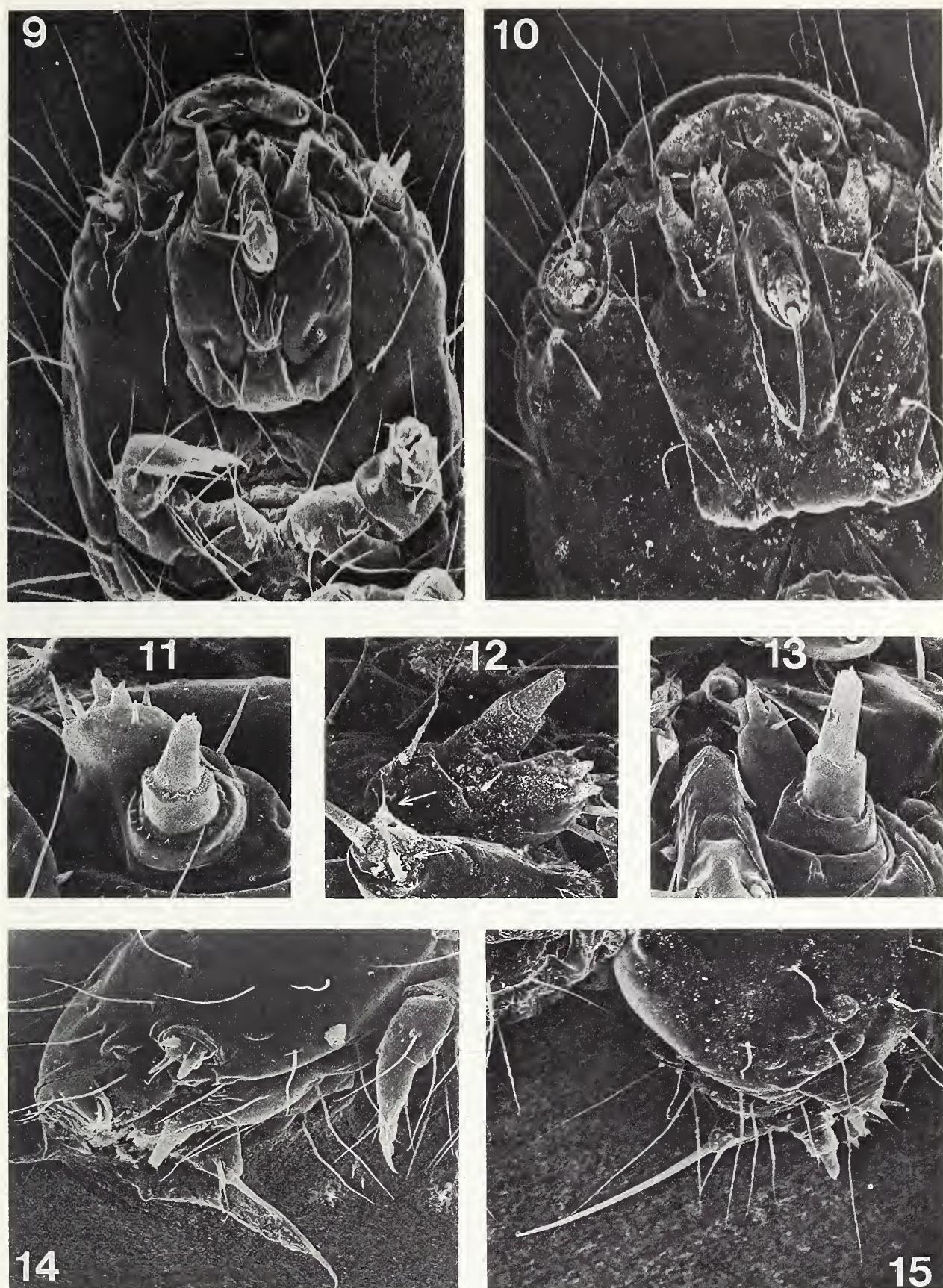


Figs. 7-8. Scanning electron micrographs. 7. Antenna of *Korscheltellus gracilis*, 1095 $\times$ . 8. Antenna of *Sthenopis auratus*, 535 $\times$ .

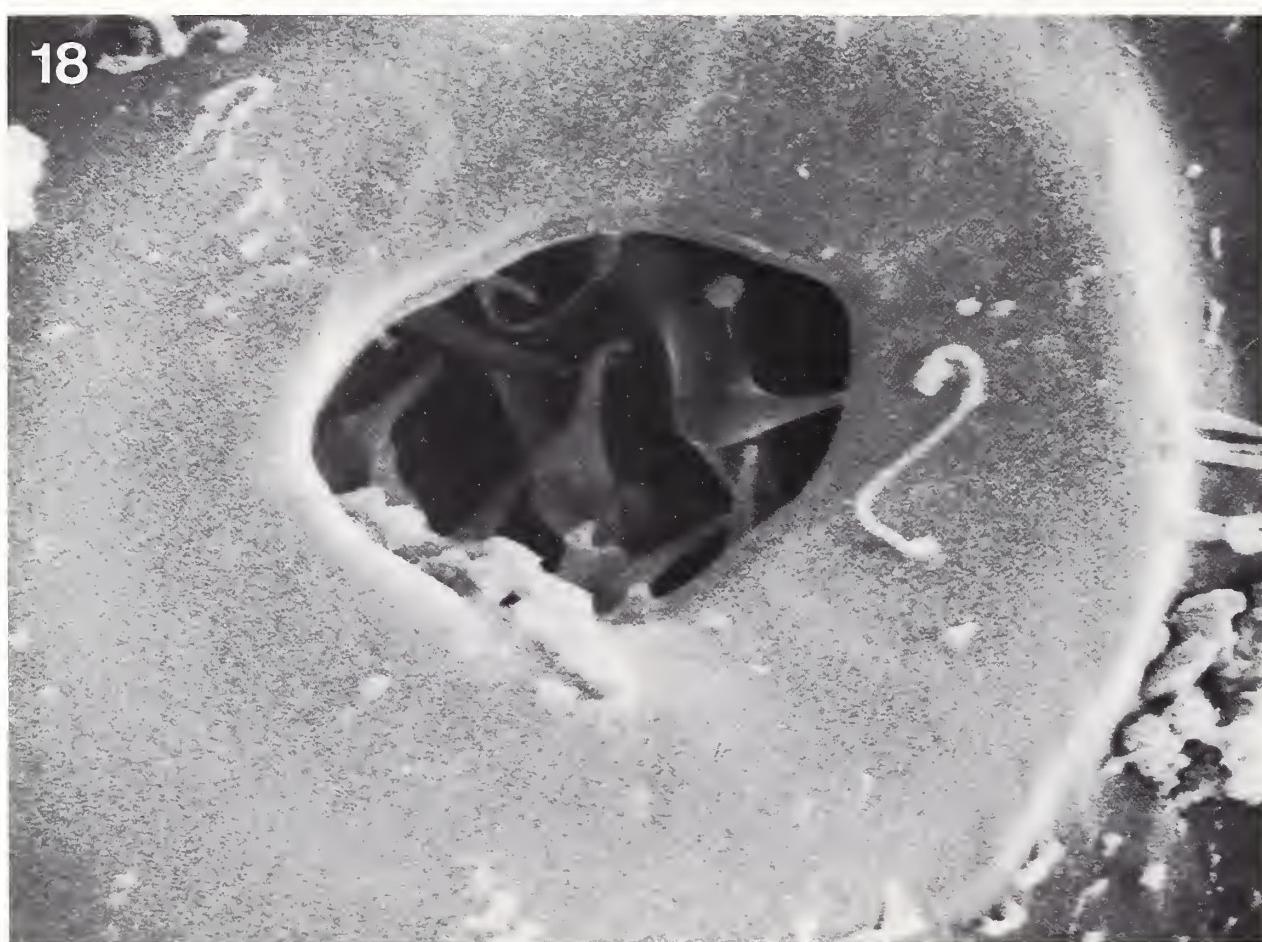
for nomenclature). First instars lack: **L2** on TII, TIII and A9; **SV2** on TII and TIII, and A7-A9; **L3** on all segments; **SV3** on A1-A9.

**Thorax.** Both species have microtrichia on all thoracic and abdominal segments but *S. auratus* is more densely covered. Conical microtrichia were present in the TI spiracular opening of *S. auratus* (Fig. 18) but absent in *K. gracilis*. The number and relative positioning of setae is the same as previously reported for other hepialid first instars. TI lateral setae (**L1**, **L2**) are on a laterad sclerotized plate just ventrad of the prothoracic shield (Figs. 19, 21). Setae **SD1**, **SD2**, and **D2** are on a thinly sclerotized latero-caudad extension of the prothoracic shield. In comparison to **D2**, setae **SD1** and **SD2** are thicker, longer and inserted into larger sockets (unlike post-first instars). **SD** setae are not subtended by dense microtrichia as in post-first instars. **D2** is closer to **SD** setae than to **XD** setae as in post-first instars. **MV** setae are of approximately equal length.

On TII and TIII of both species, **D1** pinacula are fused across the midline. Setae **D2**, **SD1** and **SD2** are on a single non-melanized pinaculum in *K. gracilis* on both TII and TIII (Fig. 19) unlike post-first instars where on TIII **D2** is on a separate melanized pinaculum (Wagner et al., 1989). In *S. auratus* **D2** is on a separate melanized pinaculum on TIII (Fig. 21), as in post-first instars (McCabe and Wagner, 1989). **MD1** is the same length as **MSD** setae in *K. gracilis* first instars which differs from post-first instars where **MD1** is longer. **MD1** in the first instar of *S. auratus* is slightly longer than the **MSD** setae. The thoracic leg claw basal tooth ends near one-

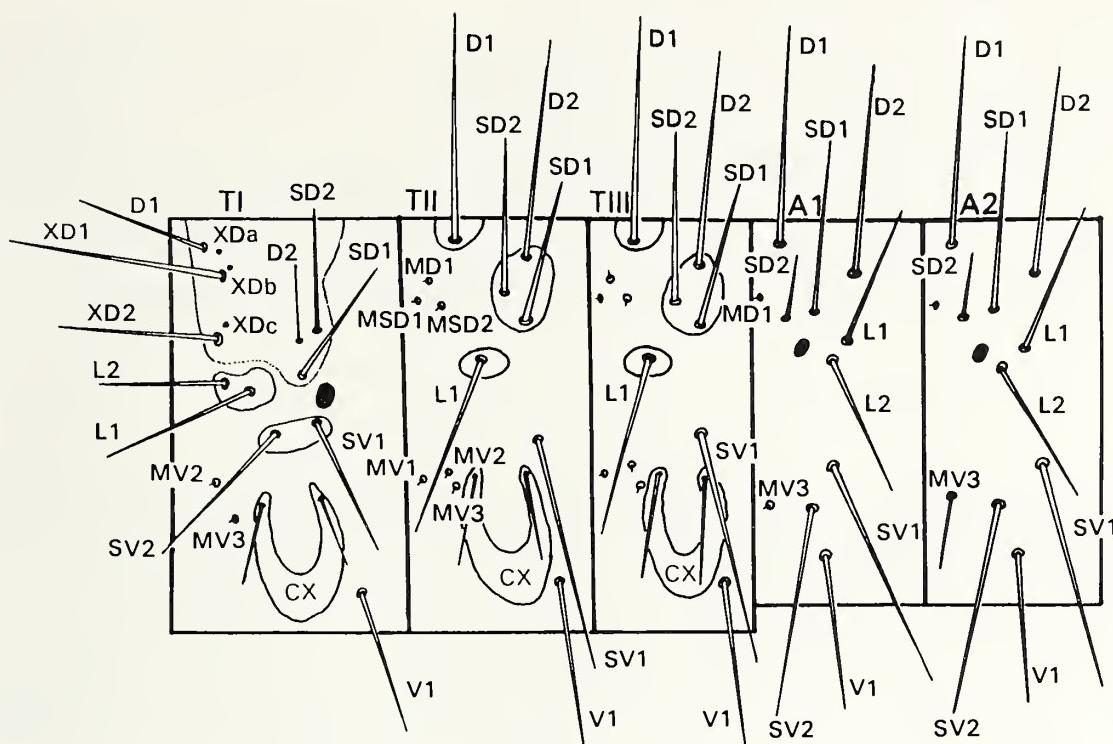


Figs. 9–15. Scanning electron micrographs. 9. Maxillolabial-hypopharyngeal complex of *Korscheltellus gracilis*, 175 $\times$ . 10. Maxillolabial-hypopharyngeal complex of *Sthenopis auratus*, 155 $\times$ . 11. Maxilla of *Sthenopis auratus*, 225 $\times$ . 12. Maxillolabial detail of *Sthenopis auratus*, 225 $\times$ . Arrows point to labial palps. 13. Maxilla of *Korscheltellus gracilis*, 465 $\times$ . 14. Head of *Korscheltellus gracilis* in lateral view, 310 $\times$ . 15. Head of *Sthenopis auratus* in lateral view, 125 $\times$ .

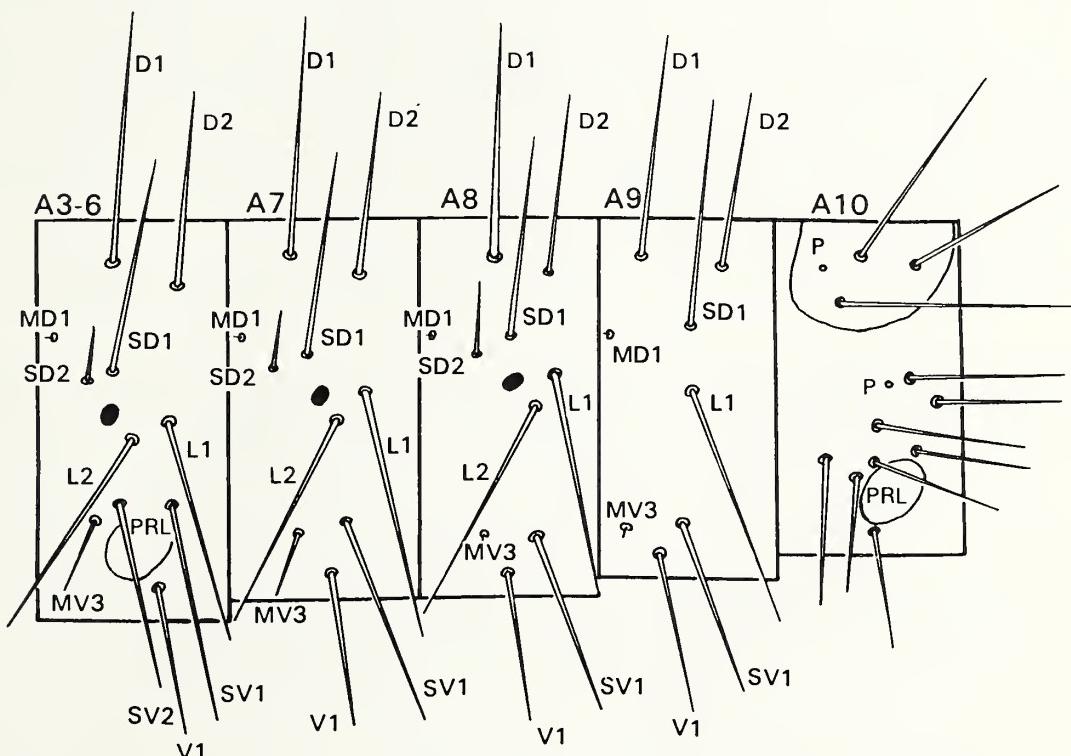


Figs. 16–18. Scanning electron micrographs. 16. Vertex setae of *Sthenopis auratus*, 145 $\times$ . 17. Detail of box from Figure 16 showing V setae. 18. Detail of spiracle of *Sthenopis auratus* showing conical microtrichia, 640 $\times$ .

19



20



Figs. 19–20. Chaerotaxy of *Korscheltellus gracilis* first instar larvae; spiracle represented by shaded ellipse. 19. Thorax and first two abdominal segments; CX, coxa. 20. Abdominal segments 3–10; non-melanized pinacula bounded by solid lines; P, pore; PRL, proleg.

third of the claw length (Figs. 23–24), but in second to final instars the tooth ends near midlength (Wagner et al., 1989: fig. 12).

**Abdomen.** The number and relative positioning of abdominal setae is the same as for other first instar hepialids. MV3 is a proprioceptor microseta on A1, A8, and A9, but a tactile macroseta on A2–A7 (Figs. 20, 22). In *S. auratus* a darkened melanized pinaculum encloses SD1 and SD2 while the L setae are each enclosed in a separate melanized pinaculum as in post-first instars. Crochets in both species are in biserial ellipses with a prominent inner row (Figs. 25, 26). Segment A10 has 11 setae and two pores: anal shield with 3 setae and a pore; remaining pore and 8 setae below shield.

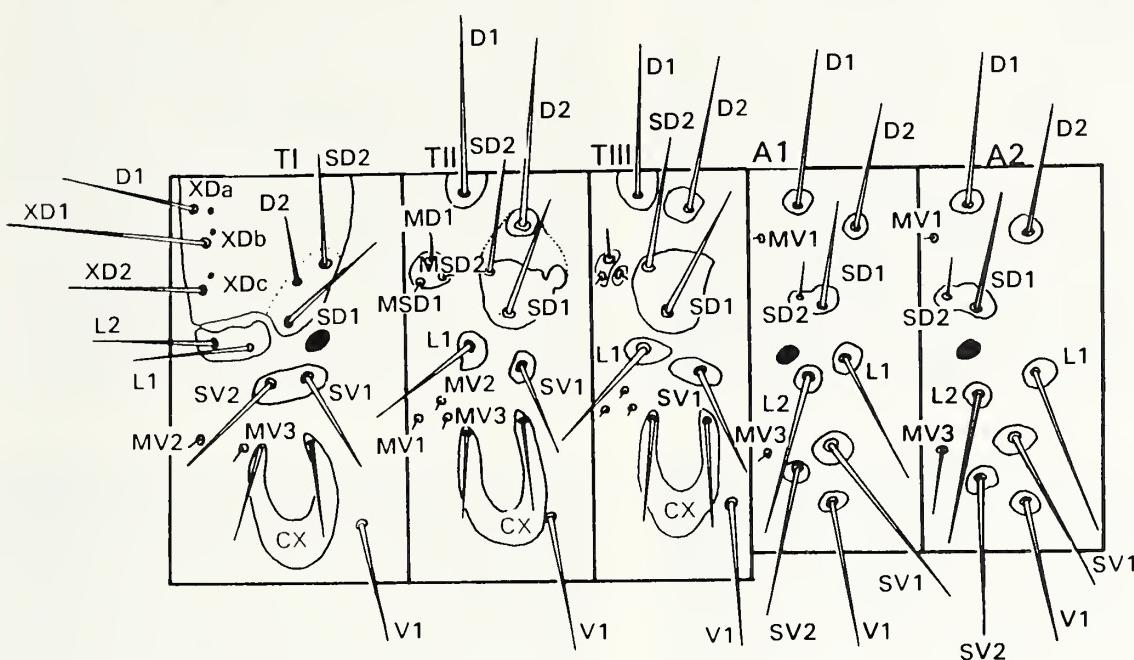
#### DISCUSSION

Chaetotaxy is important in the systematics of the Lepidoptera because it is used to distinguish taxa and to define monophyletic groups. At present there is a lack of explicit analytical criteria for identifying chaetotactic homologies that confer natural setal groups. Hinton's (1946) major review emphasized comparisons among the Ditrysia and some Monotrysia including the Hepialidae. Earlier systems were already in existence (e.g., Fracker, 1915) and Hinton's (1946) nomenclatural system modified earlier proposals by Heinrich (1916) and Gerasimov (1935) (Hinton, 1946:9, Table 1). Hinton's (1946) nomenclature has received wide application, but several authors have identified problems with respect to the Hepialidae and offered modifications (Hasenfuss, 1963, 1969; Wagner, 1987; Nielsen and Kristensen, 1989). The different alternatives and their justifications are discussed as follows:

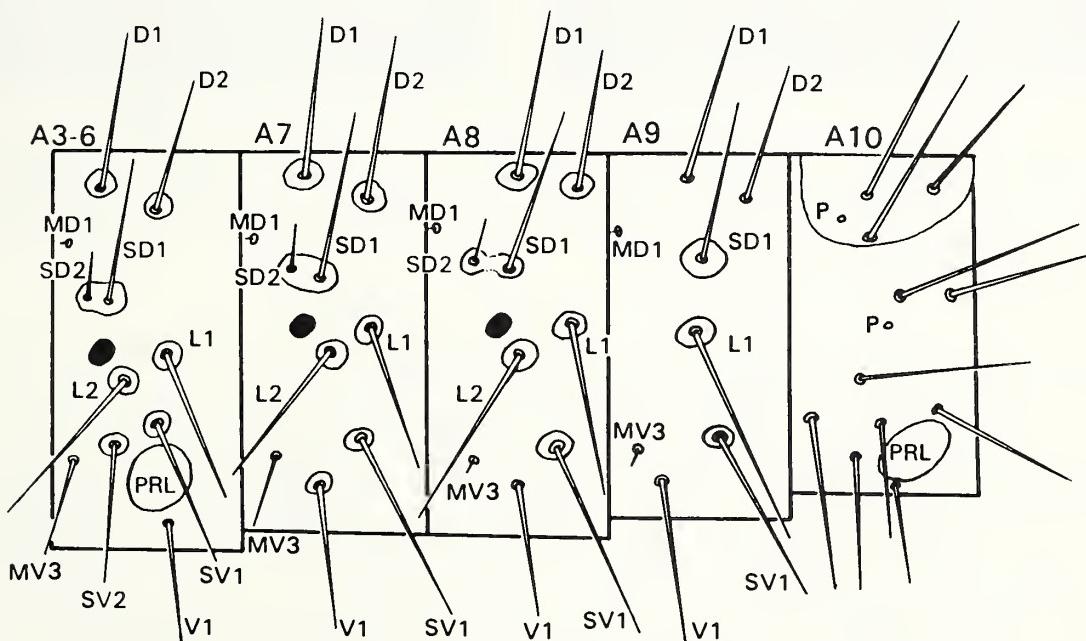
**Head.** Hinton's (1946) nomenclature (Fig. 27) was critically examined by Hasenfuss (1969), who was concerned with Hinton's designation of a unique genal micro seta (**G2**) and apparent absence of micro seta **V1** that renders the Hepialidae anomalous to the Ditrysia where **G2** is absent and **V1** is present. Hinton's (1946) contrast between Hepialidae and Ditrysia is based upon differences in size and position of setae (the **G** and **V** setal groups being defined by their small size as microsetae). Hinton (1946: 6) was unable to decide which of the **G** setae were represented in the Ditrysia and **V1** was presumed absent from Hepialidae because the two micro **V** setae present were necessarily identified as **V2** and **V3** by the interposition of the pore **Va** (Fig. 27).

Hasenfuss (1969) argued that setal length was a consequence of head capsule orientation and degree of retraction of the head against the thorax. He also pointed out that in leaf mining groups the longer tactile setae are present only on the leading edge and sides of the head capsule. He suggested that setal length alone does not qualify as a defining character (i.e., the equivalent of apomorphy) for inclusion of setae within particular setal groups. He noted that there are normally three vertex setae in the Ditrysia (**V1**, **V2** and **V3**) with the pore **Va** almost always between **V2** and **V3** (**Va** is sometimes offset to one side), while the genal region supports only a single seta **G1** (Fig. 28). While the homology of Ditrysian setae was stable, there were cases where the boundary between setal groups ("Musterelementgruppe") became blurred. Hasenfuss (1969) presented the *Yponomeuta* as an example with **V2** and **V3** present as microsetae while **V1** was very long and having the appearance of a macroseta. The Hepialidae show the same total number of head setae (although fewer

21

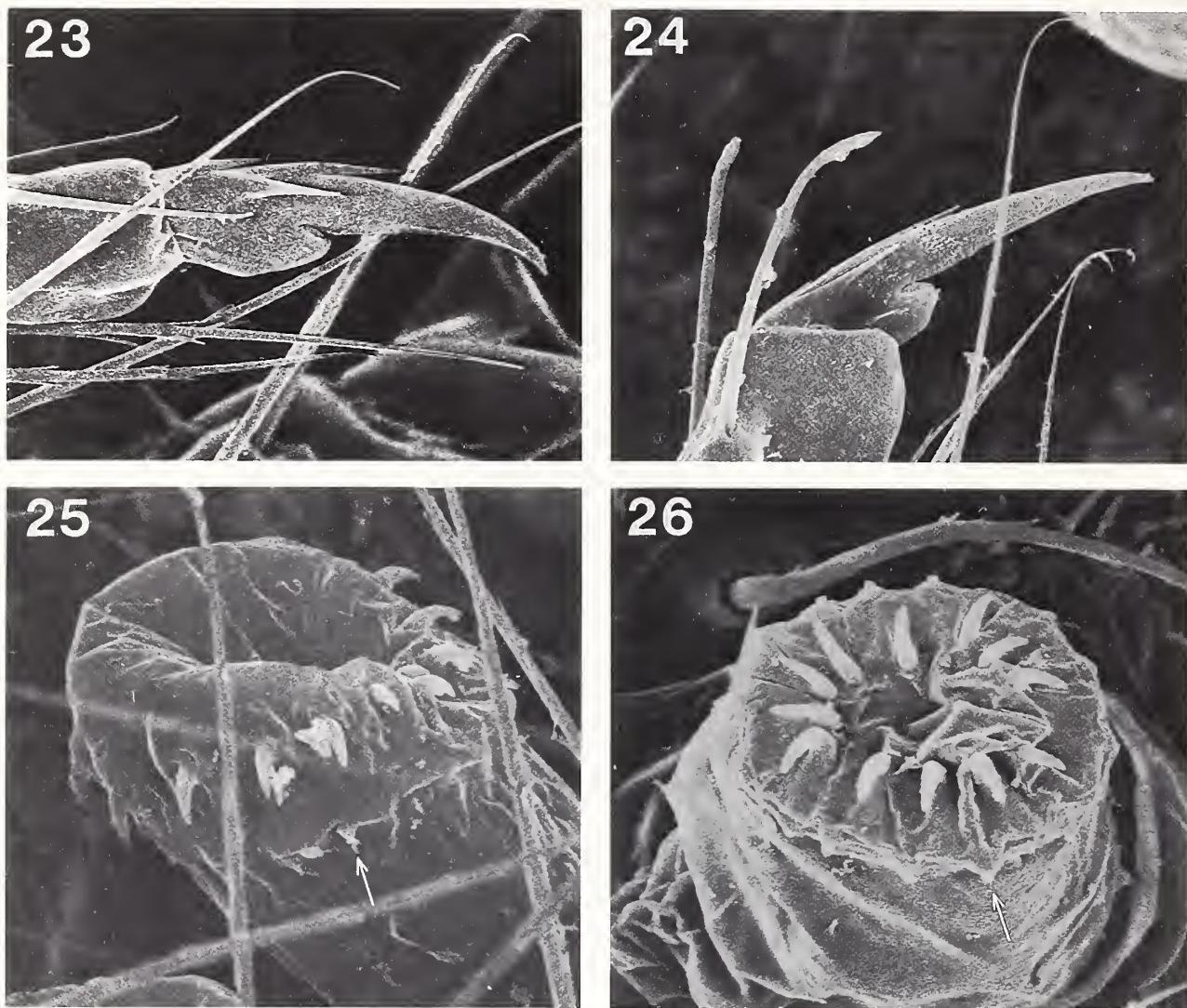


22



Figs. 21-22. Chaetotaxy of *Sthenopis auratus* first instar larvae; spiracle represented by shaded ellipse. 21. Thorax and first two abdominal segments. 22. Abdominal segments 3-10; melanized pinacula bounded by solid lines; P, pore; PRL, proleg.

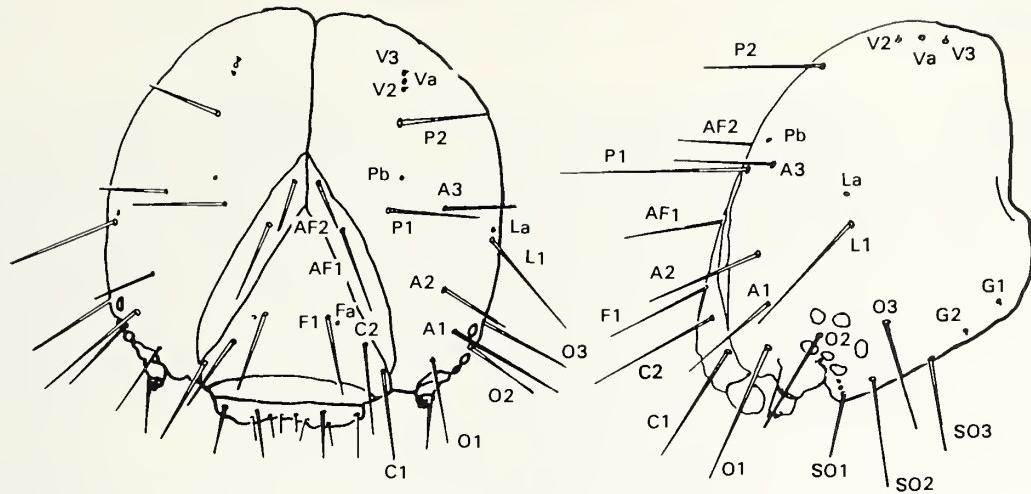
pores) as the Ditrysia, but only two microsetae occur on both the vertex (normally three in the Ditrysia), and the genal region (normally one in the Ditrysia). In Hinton's system, all the long tactile setae of Hepialidae are regarded as homologous with the Ditrysia and V1 therefore is assumed missing and a new seta, G2, considered present.



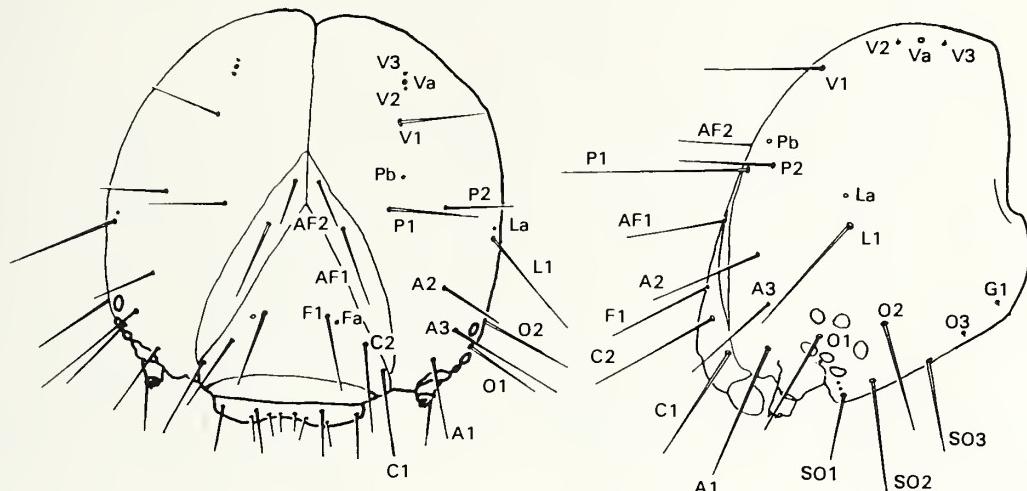
Figs. 23–26. Scanning electron micrographs. 23. Prothoracic (TI) claw of *Korscheltellus gracilis*, 1,315 $\times$ . 24. Prothoracic (TI) claw of *Sthenopis auratus*, 920 $\times$ . 25. Abdominal proleg of *Sthenopis auratus*, 820 $\times$ , arrow on outer crochet. 26. Abdominal proleg of *Korscheltellus gracilis*, 1,455 $\times$ , arrow on outer crochet.

Since *Yponomeuta* exhibits Ditrysian chaetotaxy except for the presence of only two micro-vertex setae, the macro seta anterior to V2 is necessarily V1. This arrangement of micro and macro setae is identical to the Hepialidae and, therefore, the hepialid macro seta P2 of Hinton (1946) is regarded as V1 (compare Figs. 27 and 28). Hasenfuss (1969) suggests that the resulting rearrangement supports the view that Hinton's micro seta G2 is actually homologous with O3, with the result that the chaetotaxy of the Hepialidae is identical to that of the Ditrysia.

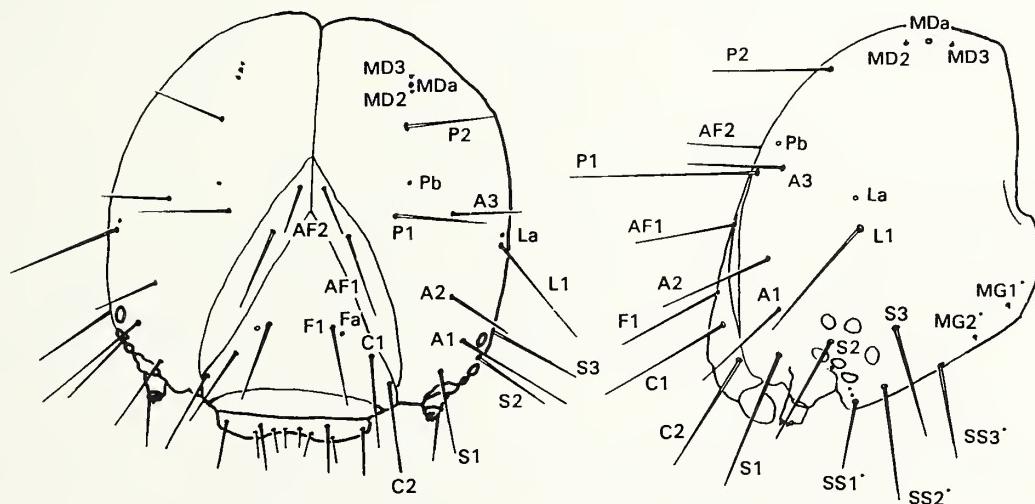
Stehr (1987) produced a system adopted by Wagner (1987) (Fig. 29) modifying Hinton's (1946) homology and terminology of the head. The major concern was that the micro-vertex setae (V series) and genal seta (G series) were proprioceptors homologous with the rest of the body and should be renamed in accordance with Hinton's system as microdorsal (MD) and microgenal setae (MG) (although to be consistent with Hinton's nomenclature, the genal setae should have been designated by MV). J. E. Rawlins (pers. comm.) suggests that while there may be some indications for homonomy of genal proprioceptors with the MV group on the thorax and abdomen, priority of usage favors retention of G and MV respectively as symbols for



**27. Hinton (1946)**



**28. Hasenfuss (1969)**



**29. Wagner et al. (1989)**

Figs. 27–29. Comparison of head chaetotaxy systems. Head of *Korscheltellus gracilis* redrawn from Wagner et al. (1989). 27. Hinton (1946) system. 28. Hasenfuss (1969) system. 29. Wagner et al. (1989) system; SS and MG setae marked with \* were not labeled in Wagner et al. (1989), Stehr (1987) system is used for these setae.

those groups. In Stehr (1987:290–291, 300) the designation of Hinton's **C1** and **C2** was accidentally reversed due to labeling error (F. W. Stehr, pers. comm.).

Nielsen and Kristensen (1989) adopted the nomenclature of Hasenfuss (1969) with the exception of the genal setae where they retain Hinton's (1946) **G2** instead of **O3** as used by Hasenfuss (1969). Kristensen (1984), in a discussion of the ground plan of the lepidopteran larval head, stated the retention of **G2** instead of **O3** "seems most natural from a phylogenetic point of view," because the genal position of the seta is ancestral in the Lepidoptera (N. P. Kristensen, pers. comm.). We have retained **O3** in this paper pending future reevaluation of cranial chaetotaxy.

The contrast between the classifications of Hinton (1946) and Hasenfuss (1969) can be represented cladistically for the **P** and **V** setae. In a cladistic representation, setae are terminals and homologies are nodes. The use of branching diagrams has no necessary implication for the ultimate origins of these morphological features although one might attempt to explore the implications with respect to ontogeny or phylogeny (Nelson, 1989).

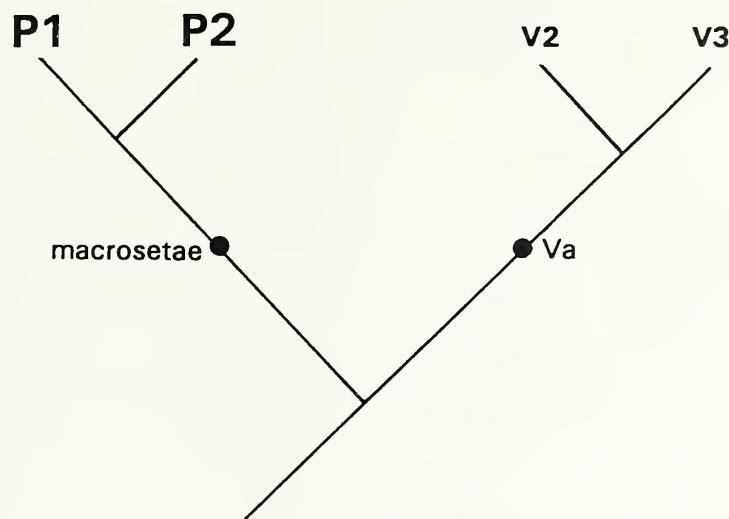
The classification of seta **P2** is inferred by Hinton (1946) to share closer relationship to the macroseta **P1** than to microsetae **V2/V3** (Fig. 30). The principles by which homologies are recognized for different setal groups were not explicitly stated by Hinton or Hasenfuss, although Hasenfuss (1963) supported a cladistic approach to phylogenetic classification in general. Hasenfuss (1969) suggested that the relative distinction between "long" and "short" setae did not provide an adequate defining character for setal groupings in this context. The fact that **P2** is long was not sufficient to place it only with **P1** because the "long" character would also place it within several other setal groups. Hasenfuss argued that the position of pore **Va** provides a defining character identifying a sister group relationship between **V3** and **V2** (i.e., the setae share a closer relationship to each other than with any other setae). To this group is added **V1** (formerly **P2**) by virtue of its position adjacent to and in line with **V2-V3** as also found in the Ditrysia (Fig. 31). With this reformulation of setal relationships, the setae of Hepialidae are not incongruent with respect to the Ditrysia and we support the nomenclature of Hasenfuss for the head capsule because the modifications are cladistically explicit and justifiable with reference to the Ditrysia. The status of **G2** also requires further clarification. The retention of **G2** by Nielsen and Kristensen (1989) while accepting **V1** of Hasenfuss requires the elimination of **O3**. We acknowledge that the present setal classifications are provisional pending future comprehensive evaluation of Lepidoptera larvae.

**Thorax.** Nielsen and Kristensen (1989) adopted Hardy's (1973) thoracic nomenclature, except for the **MD** and **MSD** microsetae where they used Hinton's system. Hardy (1973) applied a modified Hinton system but the **XD** pores on the prothorax (TI) were not labeled (Hardy, 1973:122, fig. 1). Hasenfuss (1963) reversed Hinton's subscripts for the **XD** pores so they were in linear order (a, b, c) and this order was adopted by Nielsen and Kristensen (1989). It is unclear why Hinton (1946) originally labeled these pores in the order b, a, c. He may have ordered the pores by their proximity to **XD1**. The pore labeled **XD<sub>a</sub>** is closest to the **XD1** (Hinton, 1946:19, fig. 23). We use Hasenfuss's (1963) subscripts for the **XD** pores.

Wagner (1987) adopted Stehr's (1987) system of nomenclature (which is a modification of Hinton, 1946) for the prothorax (TI), but reversed the notation of **D2** and **SD2**. The identity of Hinton's **D2** as **SD2** presents a further example of prob-

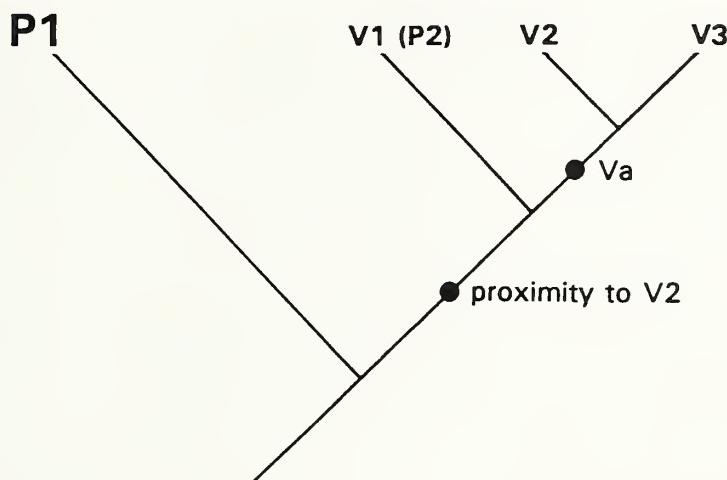
**30**

Hinton (1946)



**31**

Hasenfuss (1969)



Figs. 30–31. Cladistic representation of the vertex setae using (30) Hinton (1946) and (31) Hasenfuss (1969). Hinton's classification treats setal size as an informative character for **P1** and **P2**. This classification is altered by Hasenfuss to include Hinton's "**P2**" as part of the vertex group with the informative character being its proximity to **V2/V3**.

lematical setal relationships. Nielsen and Kristensen (1989) acknowledged Wagner's (1987) notation, but retained Hinton's usage pending further explanation of the rationale. Wagner (1987) noted that the designated **SD** setae are thin in comparison to **D2** (**SD2** of Hinton, 1946). Based on first instars, the two pronotal setae most similar in length and socket size are what Wagner (1987) calls **SD1** and **SD2** (**D2** of Hinton) (Figs. 19, 21). However, unlike post-first instars, setae **SD1** and **SD2** are thicker, longer and insert into larger sockets than **D2**.

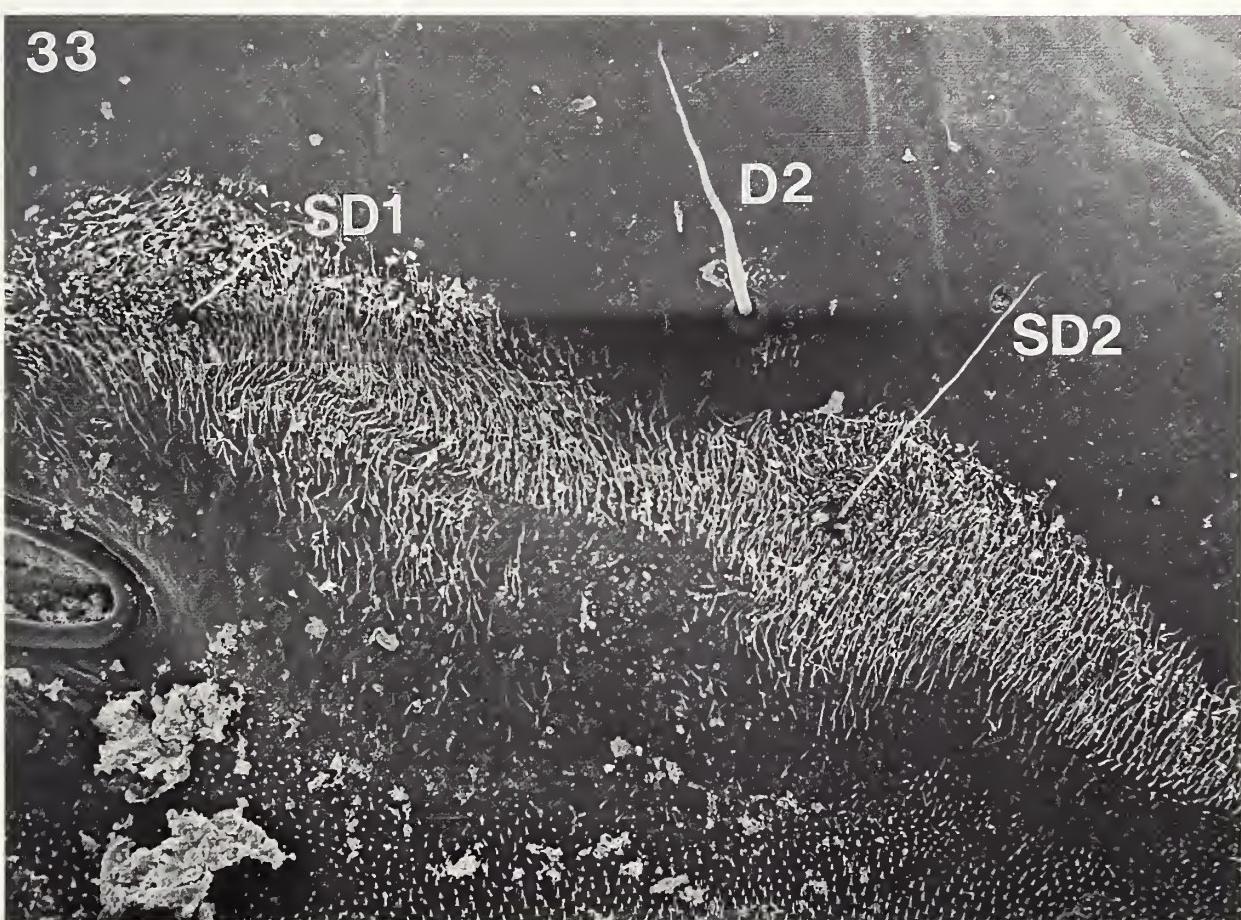
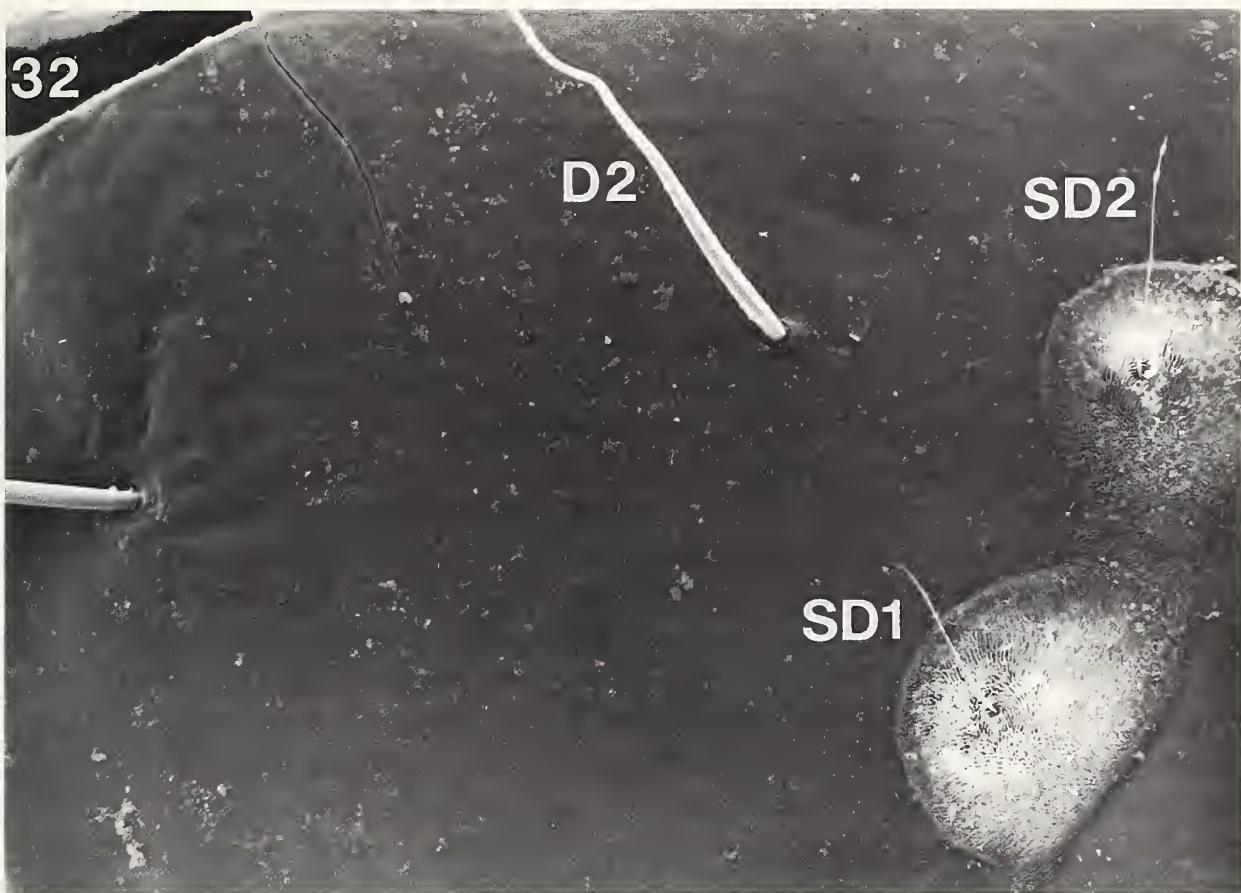
The **SD** setae (sensu Wagner, 1987) are subtended by dense microtrichia in later

instars of *K. gracilis* and *S. auratus*, as in some other Hepialidae (e.g., Fig. 32) (see also Martyn, 1960; Elder, 1978; Grehan, 1981; Nielsen and Kristensen, 1989). In still other hepialid species the seta **D2** (sensu Wagner, 1987) shares a microtrichical bed with both **SD** setae, but never with only one of them. The **SD** association with microtrichia may represent an exoporian trait as it is also present in the hepialoid sister group Mnesarchaeidae (Fig. 33) but not outside the Exoporia. Nielsen and Kristensen (1989:94) suggest that the presence of all three setae within a single “melanized depression” (=microtrichial bed of this paper) is an apomorphy for the Hepialidae sensu lato. First instar *K. gracilis* and *S. auratus* have no microtrichial bed associated with the **SD** setae or **D2** (also the case for other first instar Hepialidae), but they share a thinly melanized section of the shield. The setal size and presence of microtrichia surrounding the **SD** setae vary, but the setae consistently share homologies that exclude **D2** in all species reported and we therefore support Wagner's (1987) revision of nomenclature.

**Abdomen.** Hinton's (1946) system of abdominal nomenclature has not received modification in the literature, but requires critical examination comparable to that applied to the head capsule by Hasenfuss (1969). In particular are problems of serial homology or homonomy of the thoracic and abdominal **L** setae (D. L. Wagner, pers. comm.). Mutuura (1980) has suggested abdominal musculature as one source of characters for comparing pinacula/setal homologies between abdominal segments.

#### PHYLOGENY AND HEPIALID CHAETOTAXY

Chaetotaxy has historically provided useful phylogenetic characters, but the alternative nomenclatural choices currently available for hepialids represent a significant problem for recognizing setal homologies. Setal and pore characters currently recognized by all workers as “characteristic” for larvae of Hepialidae are based on Gerasimov (1937, 1952) and Hinton (1946) and include the following: The frons pore (**F<sub>a</sub>**) is laterad and slightly ventral to **F1** seta. The Adfrontal pore (**A<sub>fa</sub>**), anterior pore (**A<sub>a</sub>**), posterior pores (**P<sub>a</sub>, P<sub>b</sub>**), ocellar (stematic) pores (**O<sub>a</sub>, O<sub>b</sub>**) and genal pore (**G<sub>a</sub>**) are absent. Setae **A<sub>3</sub>**, **A<sub>2</sub>**, and **P<sub>2</sub>** (of Hasenfuss, 1969) are almost in line running between the stemmata and **V<sub>1</sub>**, with **P<sub>2</sub>** caudad of **P<sub>1</sub>**. Two microsetae are present in the genal region: **O<sub>3</sub>** (of Hasenfuss, 1969) and **G<sub>1</sub>**. Stemmata (ocelli) are arranged in two vertical columns. The prothoracic shield includes **L<sub>1</sub>**, **L<sub>2</sub>** and sometimes **L<sub>3</sub>** in post-first instars. The prothorax has two subventral setae (**SV<sub>1</sub>** and **SV<sub>2</sub>**) and two midventral setae (**MV<sub>2</sub>** and **MV<sub>3</sub>**). Prothoracic setae **SD<sub>1</sub>** and **SD<sub>2</sub>** (of Wagner, 1987) are diagonally positioned and thin in comparison to **D<sub>2</sub>** in post-first instars. Seta **MV<sub>3</sub>** is elongate on **T<sub>I</sub>** in post-first instar larvae. The mesothorax (**T<sub>II</sub>**) has **MD<sub>1</sub>**, **MSD<sub>1</sub>** and **MSD<sub>2</sub>** on the same pinacula anterad of **SD<sub>1</sub>** and **SD<sub>2</sub>**. Seta **MD<sub>1</sub>** is often elongate in comparison with the **MSD** setae. There is only one subventral seta (**SV<sub>1</sub>**) on **T<sub>II</sub>** and **T<sub>III</sub>**; there are two (**SV<sub>1</sub>** and **SV<sub>2</sub>**) on the prothorax. On the abdomen, setae **SD<sub>1</sub>** and **SD<sub>2</sub>** are on the same pinacula with **SD<sub>2</sub>** shorter and thinner than **SD<sub>1</sub>**. Setae **L<sub>1</sub>** and **L<sub>2</sub>** are near the spiracle with **L<sub>1</sub>** being farthest caudad and **L<sub>2</sub>** being closer and ventrad of the spiracle (**L<sub>2</sub>** is incorrectly described as being caudad of **L<sub>1</sub>** and spiracle, and **L<sub>1</sub>** ventrocaudad to spiracle in Wagner [1987]). On post-first instars, **L<sub>3</sub>** is anterad and ventrad of the spiracle on segments **A<sub>1</sub>–A<sub>8</sub>**. On segments **A<sub>2</sub>–A<sub>7</sub>**, **MV<sub>3</sub>** is elongate and grouped with the **SV** setae. Wagner (1987) identified additional hepialid larval characters: **Head:** Seta **O<sub>3</sub>** (of Hasenfuss,



Figs. 32–33. Scanning electron micrographs. 32. SD and D2 setae of *Trioxycanus* sp. showing the microtrichial bed shared by the SD setae,  $65\times$ . 33. SD and D2 setae of *Mnesarchaea* sp. showing the microtrichial bed shared by the SD setae,  $80\times$ .

1969) is approximately half-way between **G1** and **SO3**. **Prothorax: SD1** and **SD2** are diagonally positioned in a darkened pinacula. In some species **SD** pinacula encompassing **D2** in a darkened pigmented area with dense microtrichia.

Nielsen and Kristensen (1989) commented on several characters that appear to represent exoporian or hepialid apomorphies, but are also represented in other Lepidoptera. They suggest the presence of **MXD1** to be a glossatan groundplan character, and its absence an Exoporian groundplan trait (but not a synapomorphy since this proprioceptor is found in some but not all Eriocraniidae). Wagner (1987) identified the presence of two microgenal setae on the head as unique characteristics of Hepialidae, but this does not apply using the classification of Hasenfuss. Adult Hepialidae provide only one recognized synapomorphy (absence of tibial spurs) and this is not a universal character for the Hepialidae sensu lato (Viette, 1949; Wagner and Tindale, 1988; Nielsen and Kristensen, 1989:113). The cladistic status of many chaetotactic characters recognized for the Hepialidae require clarification. A cladistic classification of setae, as proposed in this paper for the V series, provides a measure of confidence for comparative chaetotaxy and may help determine which setal characters qualify as hepialid synapomorphies. Complementary to this kind of evaluation is the inclusion of a greater range of larval records, including first instars which are extremely easy to obtain from fertilized eggs.

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**A NEW SPECIES OF *ORCYA* FROM THE MARONI  
RIVER BASIN OF FRENCH GUIANA  
(LEPIDOPTERA: LYCAENIDAE)**

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*Abstract.*—First report of pan-Neotropical *Orcya* from the Guyana Shield is *Orcya snyderi*, a distinctive new species described from recently disturbed riparian rain forest margin, upper Maroni River, French Guiana. Sister genus *Noreena* has a regional endemic of similar distribution.

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I recently revised the Neotropical “*Thecla orcynia* Group” (Draudt, 1919) placing twelve pan-Neotropical species in the new genus *Orcya* (Johnson, 1990) and related this genus to a number of sister- and outgroups by numerical cladistic analysis (Johnson, 1989a, 1990). No member of *Orcya* was known from the Guyana Shield region, though a species endemic to this area occurs in a sister genus (*Noreena guianivaga* Johnson) (Johnson, 1989a, b).

Calvin Snyder (volunteer field worker, American Museum of Natural History [AMNH]) recently returned from extensive field work along the Maroni River in French Guiana and his collections included a female of a distinctive new species of *Orcya*. Subsequently, a male and five females from French Guiana were located at the Museum National d’Histoire Naturelle (Paris) (MNHN). This new species is described below, following on the generic diagnosis of *Orcya* (Johnson, 1990). For brevity, the abbreviations DFW, DHW (dorsal fore- and hindwings) and VFW, VHW (ventral fore- and hindwings) are used.

***Orcya snyderi*, new species**

Figs. 1, 2

**DIAGNOSIS.** Male dorsal iridescence limited on FW to baso-medial cells CuA1–CuA2, HW to centro-medial patch; female DFW, DHW non-iridescent dark gray (congeners brightly iridescent in both sexes). Unique pattern elements: (1) DHW black marginal band basad of greatly elongate tails (terminus vein CuA2), (2) VFW, VHW each with (i) prominent black submarginal band, (ii) black medial band (costa to cell M3) basad of, and broadly paralleling, usual white wing band of genus. Male genitalia with diminutive, elliptically shouldered valvae and thin, elongate, vincular structures; female genitalia with anterior and posterior elements of ductus bursae both undulate.

**DESCRIPTION.** *Male.* Upper surface of wings: DFW lacking androconial brand as typical of genus, FW with dark azure blue iridescence confined to baso-medial areas of cells CuA1–CuA2 and to a centro-medial HW patch; tails on known specimen broken (short tail apparent only at terminus vein CuA2, see Female below), anal lobe with bold orange spot. Under surface of wings: ground dark gray, FW with faint

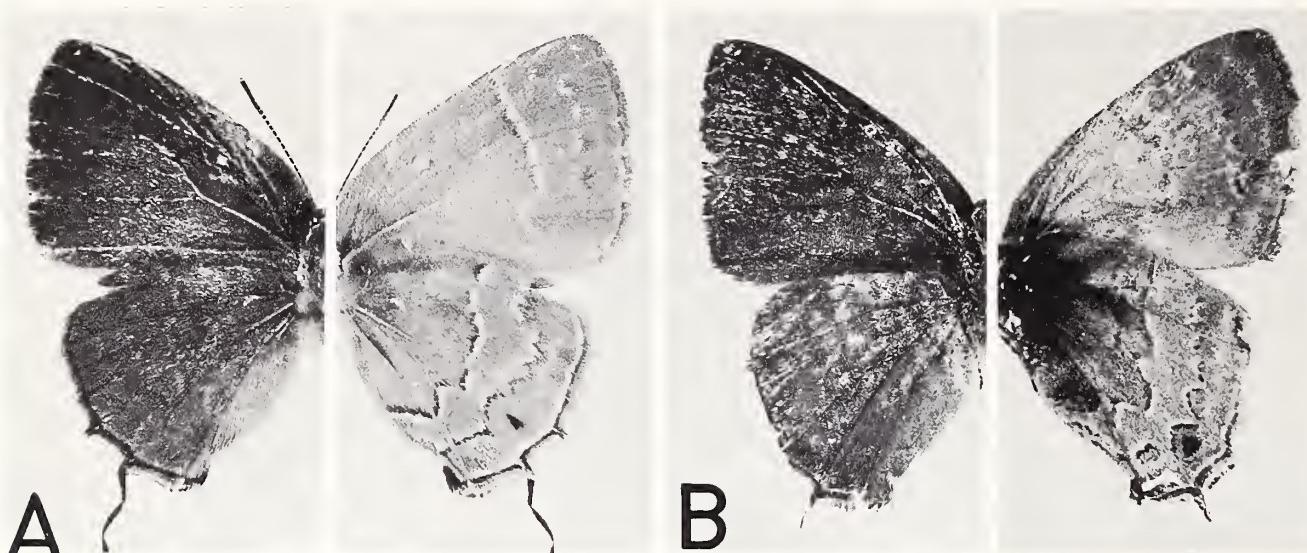


Fig. 1. Adults of *Orcya snyderi*, new species. A. holotype female (upper surface, left; under surface, right). B. allotype male (same view).

black postmedial and submarginal bands (known specimen worn); HW with basal area charcoal gray with slight white slash in discal cell, medial area with meandering white band, broadly bordered basally with black, angled in wide "W"-shape before the anal margin; submarginal area with jagged white band bordered distally with black extending from costa to anal margin and surrounding submarginal orange spots in cell CuA1 and at base of anal lobe. Length of forewing: 11.5 mm (allotype).

*Female.* Upper surface of wings: ground dull gray, FW margins and apices black, HW with black marginal line; HW margin with short black tail, terminus vein CuA1, elongate white-tipped black tail, terminus vein CuA2, anal lobe at anal margin with bold orange spot. Under surface of wings: ground gray, FW with (i) white postmedial line, bordered basally by black, extending in straight line from costa to cell M3 then basally angled to inner margin; (ii) white submarginal line, bordered basally with black, extending in an arc from costa to cell M3 (see Remarks); HW with (i) medial band distally white, basally black, arched widely from costa to cell M3, thereafter jagged in wide "W"-shape before anal margin; (ii) finely jagged, basally white-suffused, black submarginal band extending from costa to anal margin and surrounding submarginal orange orbicular markings in cell CuA1 and at base of anal lobe. No white discal slash that typifies other species of genus. Length of forewing: 11.5 mm (holotype); 11.5–12.5 (× 11.9) (five paratypes).

*Male genitalia.* Figure 2B. Generally typical of genus (Johnson, 1990: figs. 6, 8) but with ventral vincular parts elongate, slim; valval ventrum parabolic in bilobed area (2B,a,1), terminating in relatively short tapered caudal extensions (2B,a,2). Aedeagus elongate, exceeding rest of genitalia length by about two-fifths; caecum comprising about one-fourth aedeagal length.

*Female genitalia.* Figure 2A. Generally typical of genus (Johnson, 1990: figs. 7, 9) but distinctive as follows: anterior and posterior elements of ductus bursae undulate, length of former about one-half that of latter, posterior element with produced ventral lip; cervix bursae with hood more prominent than in congeners; corpus bursae with paired signa more robust and terminally pronged than in any congener.

**TYPES.** Holotype female (Fig. 1A), FRENCH GUIANA, Maripasoula; environs

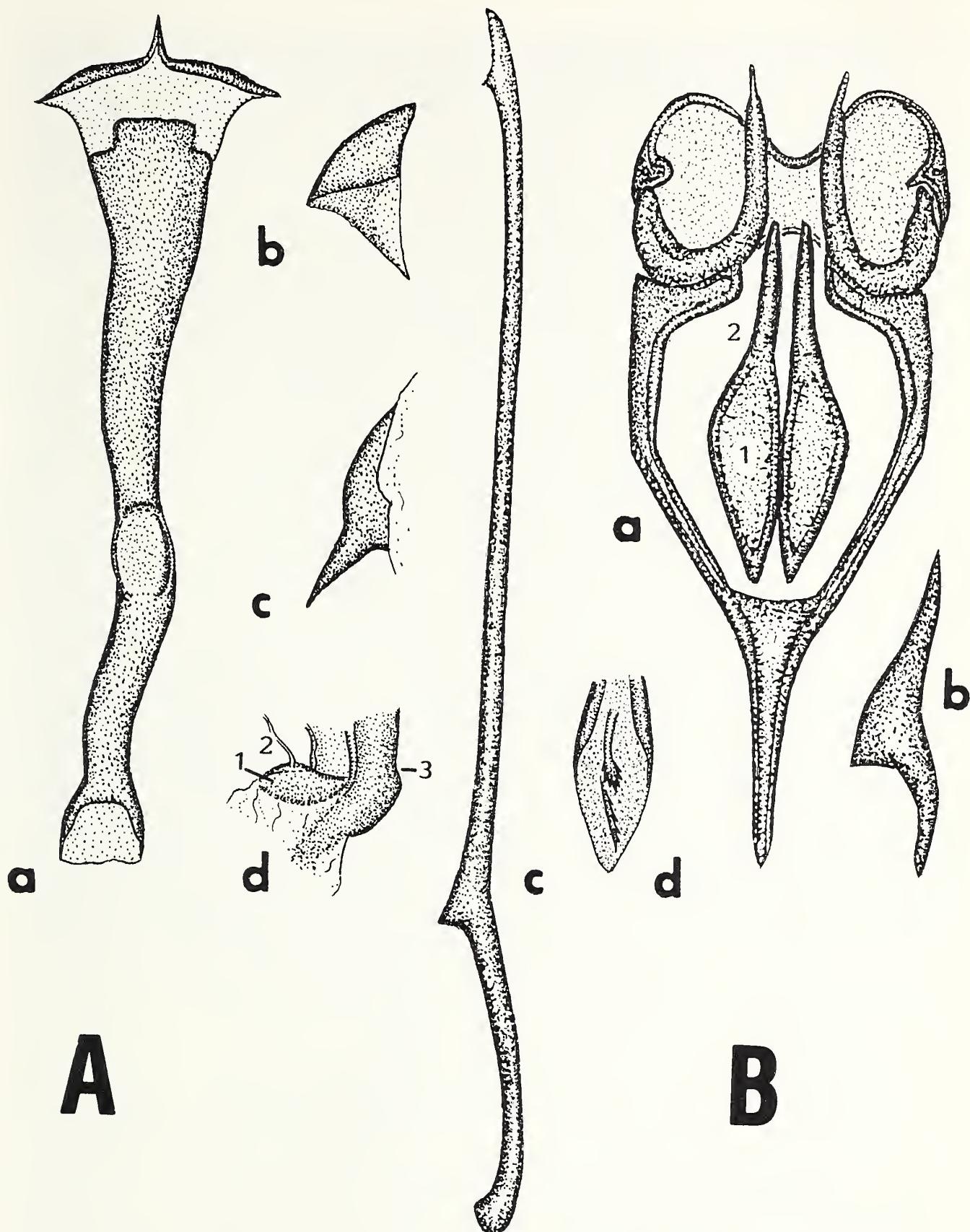


Fig. 2. Genitalia of *Orcya snyderi*, new species. A. holotype female: a, ductus bursae, ventral view; b, lamellar keel, lateral view; c, corpus bursae signum, lateral view; d, cervix bursae [1] with adjoining ductus seminalis [2] and anterior terminus of ductus bursae [3], all in lateral view. B. allotype male: a, genitalia with aedeagus removed (valval bilobed area [1], caudal extension [2]), ventral view; b, valvae, lateral view; c, aedeagus, lateral view; d, aedeagus terminus, ventral view.

of Maripasoula, 125 m, 31 March 1991, leg. C. Snyder, deposited AMNH. Allotype male (Fig. 1B) labelled "Guyane Francaise, Rives [=“banks of”] de Maroni, E. Le Moult 1909," deposited MNHN. Paratypes. MNHN: five females labelled "Guyane Francaise, Rives de Maroni, E. Le Moult 1909" (2) and "Guyane Francaise, Maroni, E. Le Moult 1909" (3).

DISTRIBUTION. Currently known from the Maroni River basin in French Guiana/Surinam (see Remarks).

REMARKS. *Habitat.* Only the holotype has precise field data. Snyder (pers. comm.) reports that the specimen was collected in the morning in moist secondary riverbank forest and scrub, in an area of high annual rainfall (up to 3,000 mm) broken by a 2½ month dry season. Time of collection coincided with the so-called "March summer" of the region, a period of scant rainfall at the midpoint of the November to July rainy season. Before disturbance the habitat supported lowland rain forest typical of the Guyana Shield on both sides of the river (the east bank now being in Surinam).

*Orcya snyderi* and historical names in "Thecla." Because wing markings of the *O. snyderi* female might be construed as resembling the short original description ("OD") of *Thecla imma* Prittwitz (1865), explanation is needed concerning why I do not associate this name with *Orcya*. *Thecla imma* was described from a single female, now lost, from Corcovado, Rio de Janeiro, Brazil (Bridges, 1988) and the name has been variously applied by curators and catalogers. Draudt (1919) placed *T. imma* in his *Thecla* "strophon-Group," a diverse assemblage of species showing a wide "W"-shaped bend in the VHW band and reduced DFW structural color (Draudt, 1919, pl. 151d-g). Draudt (1919:781) also noted similarities between the OD of *T. imma* and members of his "orcynia-Group," some of which I included in *Orcya* (Johnson, 1990). Early lycaenid specialists W. P. Comstock and E. I. Huntington, curating at the AMNH, attached the name *T. imma* to a variety of Central and South American specimens (some of the latter noted as "new species nr. *imma*"). I included morphological data from these specimens in data matrices for numerical cladistic analysis (Johnson, 1989a, 1990). The final rooted tree (Johnson, 1989a, fig. 8; 1990, fig. 1) included some South American specimens as "undescribed Outgroup X" (Johnson, 1989a, = "Group 3" Johnson, 1990). The other specimens, including the Central American ones, were rejected from the *Orcya* ingroup and placed with specimens of *Thecla orios* Godman & Salvin (1879–1901 [1887]) based on characters of its holotype, a Guatemalan male (Johnson, 1990 "Group 1," an outgroup at the base of the cladogram). I thus consider "*Thecla imma*" objectively ambiguous, its OD being applicable to any number of specimens of divergent morphology. It is particularly noteworthy that an arbitrary application of *Thecla imma*, based on its OD and a regional view of its type locality, would likely include specimens of either "Outgroup X" or *Contrasacia* Johnson (1989a). As can be seen from figure 7A–C in Johnson (1989a), the morphology of these latter groups differs greatly from that of *O. snyderi* and its congeners discussed below. I have proposed elsewhere (Johnson, 1991a) that certain widely used historical names, ambiguous in a revisionary context, may eventually require formal suppression under the ICZN Code.

*Intrageneric relations.* Distinctive characters in both the male and female of *O. snyderi* are intriguing. Unique wing characters include: (1) reduced and absent DFW, DHW surface structural color in males and females, respectively; (2) bold under surface submarginal bands on the fore- and hindwing; (3) small size (congeners

generally 13.5–17.0 mm [15.0–17.0 mm in the common and widespread taxa, 12.0–14.0 mm in the few austral species]). Because of these characters, *O. snyderi* is not readily associated with the genus from a superficial view.

Features appearing somewhat like other congeners require careful consideration. The distinctive VHW pattern, for instance, cannot be considered informative. Austral species *O. larseni* (Lathy) and *O. obliqua* Johnson also have VHW medial bands departing from the thin, extremely jagged pattern typifying most of the genus but neither species' band resembles the robust band of *O. snyderi*. Similarly, southeastern Brazil xerophile *O. catharina* (Draudt) shows reduction of the VHW discal slash but it is never completely absent in fresh specimens as is the case in *O. snyderi*.

Truly compelling similarities involve other wing characters and some structural features emphasized by Johnson (1990) in the generic analysis. Most prominent are several wing and genitalic characters shared by *O. snyderi*, *O. hewitsoni* Johnson (humid montane forest, northern Ecuador south to central Peru) and *O. anthracea* (Hewitson) (humid montane forest, southeastern Brazil). These three taxa show bold hindwing medial bands marked near the anal margin with an emphatic "W"-shaped element and bright orange orbs. In the female genitalia the ductus bursae is undulate and the respective anterior and posterior elements of similar size. Typifying the tendency toward autapomorphy in male genitalia of *Orcya* (Johnson, 1990, figs. 6, 8), details in *O. snyderi* (ventral valval and vincular shape, elongate aedeagus) do not argue for or against any particular intrageneric relation.

**Biogeography.** Affinity of *O. snyderi* to *O. hewitsoni* and *O. anthracea* mirrors biogeographic relations in several other groups of butterflies where the Amazon basin segregates sister species into respective Guyana Shield, western Andean, and south-east Brazilian distributions. This pattern occurs in sister genus *Noreena* (Johnson, 1989a) and numerous other Theclinae (Johnson, 1991a, b). Regarding an Andean/Maroni River basin sister species relationship, perhaps the most oft-cited example is *Heraclides maroni* (Moreau) and *H. rhodostictus* (Butler and Druce) (Papilionidae), where the superficial resemblance is so striking that first reported specimens of the former were thought to be mislabelled examples of the latter (D'Abrera, 1981; Johnson and Rozycki, 1986; Johnson and Matusik, 1989).

**Etymology.** Patronym for Calvin Snyder who collected the holotype.

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## NOVEL TAXA OF *TRICHOGRAMMA* FROM THE NEW WORLD TROPICS AND AUSTRALIA (HYMENOPTERA: TRICHOGRAMMATIDAE)

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*Abstract.*—Three new species of *Trichogramma* from the New World tropics and one new species from Australia are described. These taxa differ from all congeners by the unjoined funicular and club segments of the male antenna, and the two-segmented maxillary palp. The New World species also are distinguished by the unique structure of the aedeagus. All four new species are retained tentatively within the nominate subgenus of *Trichogramma*. Their relationship to other species of the genus is discussed.

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The study of recent Trichogrammatidae collections from the Neotropics and Australia has revealed four new species of *Trichogramma* which extend considerably the known anatomical variation in this cosmopolitan genus of insect egg parasitoids. These species share certain derived features that define *Trichogramma*, but are believed to represent primitive lineages that diverged before the attainment of fusion of the antennal flagellomeres in males. Pending an evaluation of phylogenetic relationships in the genus these taxa are tentatively placed in two informal species groups within the nominate subgenus, the Lachesis and Primaevum groups.

In this paper the new species groups and included species are described. These taxa are compared to other elements of *Trichogramma*, and their phylogenetic position and taxonomic treatment are discussed. Also, terms are utilized for the male genitalia that conform to those adopted for other genera of Trichogrammatidae.

### TERMINOLOGY

The male genitalia comprise the most important character complex in *Trichogramma*. Species identifications were virtually impossible prior to Nagarkatti and Nagaraja (1968) in which this rich source of variation was first considered. Because of questions of homology, however, these authors introduced a unique terminology for certain genitalic structures in *Trichogramma* and *Trichogrammatoidea* (Nagarkatti and Nagaraja, 1968, 1971, 1977; Nagaraja, 1978). This was adopted by other authors (e.g., Ertle and Davis, 1975; Pinto and Oatman, 1985; Pinto et al., 1978, 1989; Schulten and Feijen, 1978, 1982; Vincent and Goodpasture, 1986; Voegeler and Pintureau, 1982) and became standard in studies of both genera. In contrast, Viggiani (1971), and Viggiani and Laudonia (1989) utilized a terminology for all Trichogrammatidae which stems from generalized works on Hymenoptera genitalia (Snodgrass, 1941, 1957; Domenichini, 1953). This is largely employed here, and it is suggested that other investigators working with *Trichogramma* and *Trichogrammatoidea* also adopt these more conventional terms. Maintaining two distinct terminologies within the family is awkward and potentially confusing.

The descriptions of male genitalia in the new species treatments, for the most part, are consistent with Viggiani and Laudonia (1989). The structures, acronyms (also see Figs. 10, 11, 13) and, where appropriate, counterparts (in brackets) used by Nagarkatti and Nagaraja (1968, 1971) are as follows:

Genital capsule (GC)—the entire genitalia except the aedeagus; phallobase (PB) [=gonobase, GB]; dorsal aperture of the phallobase (DA); dorsal lamina (DLA) [=dorsal expansion of gonobase, DEG & DEGB]; parameres (PM) [=gonoforceps, GF]; volsellar digiti (VS) [=chelate structures, CS]; intervolsellar process (IVP) [=median ventral projection, MVP]; intervolsellar bridge (IB)—surface between the base of the volsellae, includign the IVP; ventral ridge (VR) [=chitinized ridge, CR]; ventral processes (VP)—paired papillae or tubercle-like structures lateral to the ventral ridge, at or near base of IVP [=lateral tubercles (Nagaraja, 1978), and paired ventral protuberances (Nagaraja and Nagarkatti, 1969)]. GC, IB, VR and VP were not considered by Viggiani and Laudonia (1989).

Acronyms terminating with L, D or W signal length, distance and width measurements, respectively. Included are HTL (hind tibial length), FWW (maximum forewing width), FWL (forewing length, taken from tegula to wing apex), GW (maximum width of genital capsule), GL (maximum length of genital capsule), AD (apical distance of genital capsule: from base of volsellae and IVP to apex of PM), BD (basal distance of genital capsule: GL minus AD, or distance from base of volsellae and IVP to base of genital capsule), AL (length of aedeagus, including apodemes), OL (maximum length of ovipositor).

Acronyms for two types of sensilla on the antenna are BCPS (=basiconic peg sensilla), and PS (=linear, placoid sensilla). Sensilla formulae in descriptions refer to these sensilla on each of the funicular and club segments. Funicular and club segments are referred to as F1–2, and C1–3, respectively.

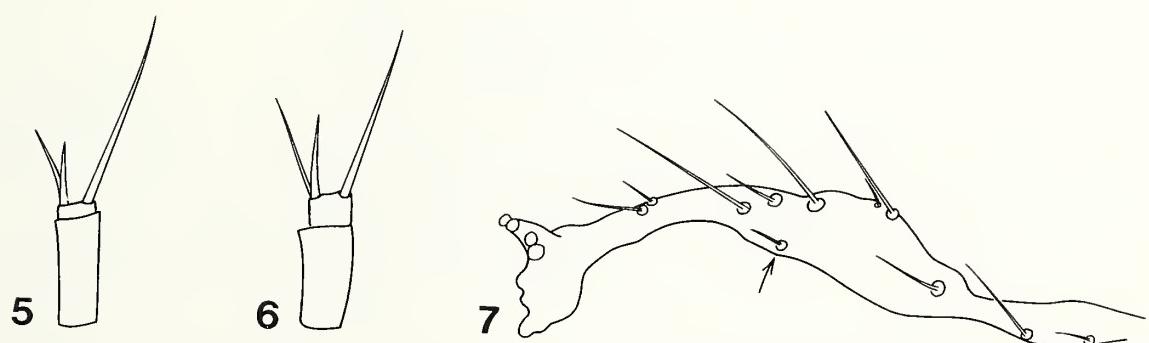
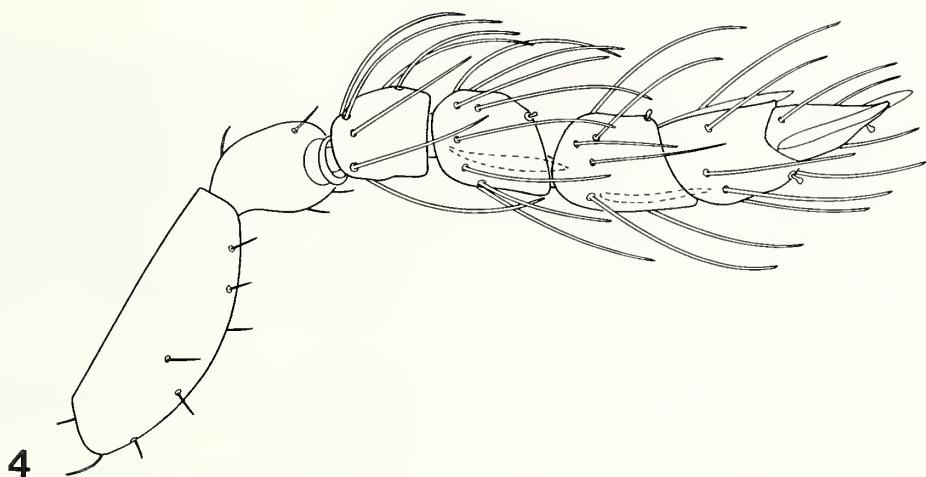
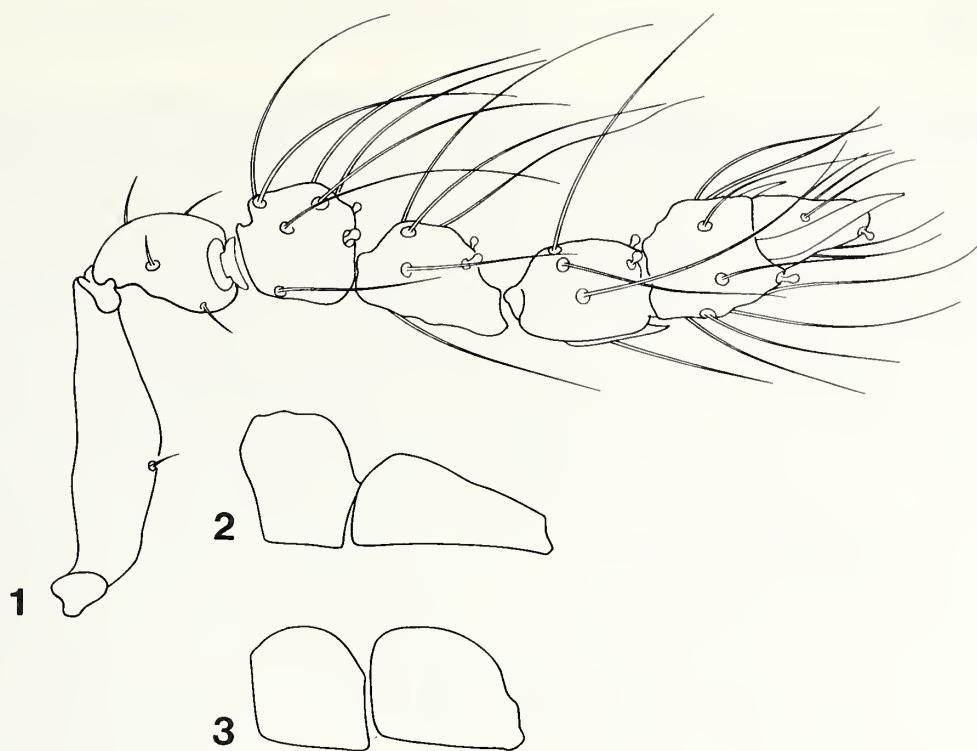
Antennal, forewing and genitalic features referred to in the descriptions are illustrated below. Hindwing and scutellar features are illustrated in Pinto et al. (1978).

#### DEFINING FEATURES OF *TRICHOGRAMMA*

*Trichogramma* is easily distinguished from other Trichogrammatidae. The forewing is relatively broad with distinct vein tracks including an RS<sub>1</sub>; the stigmal vein is well developed but not abruptly delimited from the marginal vein—instead it gradually curves into the latter, resulting in the characteristic “sigmoid” venation (Fig. 7). The female antenna consists of two funicular segments and a single club segment. The male genitalia have a dorsal lamina and the aedeagus is not fused to the genital capsule.

*Trichogramma* is believed to be closest to *Trichogrammatoidea* (Nagarkatti and Nagaraja, 1977; Nagaraja, 1978). They share the “sigmoid” venation in the forewings, the antennal structure of females is identical, and they have similar male genitalia. Although similar, *Trichogrammatoidea* lacks the RS<sub>1</sub> vein track in the forewing as well as the dorsal lamina of the genital capsule. The latter feature, so far as known, is unique in the family (see Viggiani 1971, 1984) and is the derived feature defining *Trichogramma*.

Until now, *Trichogramma* was also distinguished from *Trichogrammatoidea* and other genera by its male antenna. In *Trichogrammatoidea* the two funicular and three club segments are distinct. In virtually all species of *Trichogramma*, these five seg-



Figs. 1–7. Male antennae, maxillary palp, and forewing venation in the Lachesis and Pri-maeum groups of *Trichogramma*. 1. *Trichogramma lachesis*, antenna (left). 2. *Trichogramma cloTho*, funicle. 3. *Trichogramma atropos*, funicle. 4. *Trichogramma primaevum*, antenna (left). 5. *Trichogramma lachesis*, maxillary palp. 6. *Trichogramma cloTho*, maxillary palp. 7. *Trichogramma lachesis*, forewing venation (arrow points to submarginal seta).

ments, as well as the second anellus, are consolidated into a single, elongate segment. The only previous exceptions known were species in the subgenus *Trichogramma* Carver which has the two funicular (but not the club) segments unjoined (Carver, 1978; Oatman and Pinto, 1987).

The four new species described below necessitate a modest redefinition of *Trichogramma*. In these species, forewing venation and vein tracks, and male genital structure (with the dorsal lamina) are typical of the genus. However, unlike all congeners, the two funicular and three club segments are unjoined as in *Trichogrammatoidea* (Figs. 1, 4). In addition, the maxillary palp is two-segmented (Figs. 5, 6). In all congeners, as well as in *Trichogrammatoidea*, the palp is one-segmented. It should be noted that although the number of flagellomeres in these new species agrees with *Trichogrammatoidea*, antennal structure (e.g., shape, sensilla type and number) does not. Instead, in all respects, their antennae more closely resemble other trichogrammatine genera, particularly *Australufens* and *Trichogrammatomyia*. For example, the club is compact, suboval in shape, and C3 is subconical and pointed apically. In *Trichogrammatoidea* the club is more elongate, the segments are more loosely joined, and C3 is rounded apically (Doutt and Viggiani, 1968). The phylogenetic implications of these new species and the justification for placing them in species groups in the nominate subgenus is discussed following the descriptions.

#### LACHESIS GROUP

As in other *Trichogramma* except as follows: Male antenna with two funicular and three club segments; C3 subconical, pointed apically; funicular segments lacking linear PS. Aedeagus (Fig. 12) apparently bilobed with phallotreme more extensive than in congeners, extending a distance from apex along ventral surface; aedeagus longer than genital capsule. Maxillary palp two-segmented (Figs. 5, 6). Forewing with a seta near posterior border of marginal vein (Fig. 7). Hindwing without a posterior vein track.

*Notes.* The Lachesis Group contains three species from Central America and northern South America. The female is indistinguishable from congeneric females except for the structure of the maxillary palp, and wing setation.

*Etymology of specific names.* After the three Fates of Greek mythology.

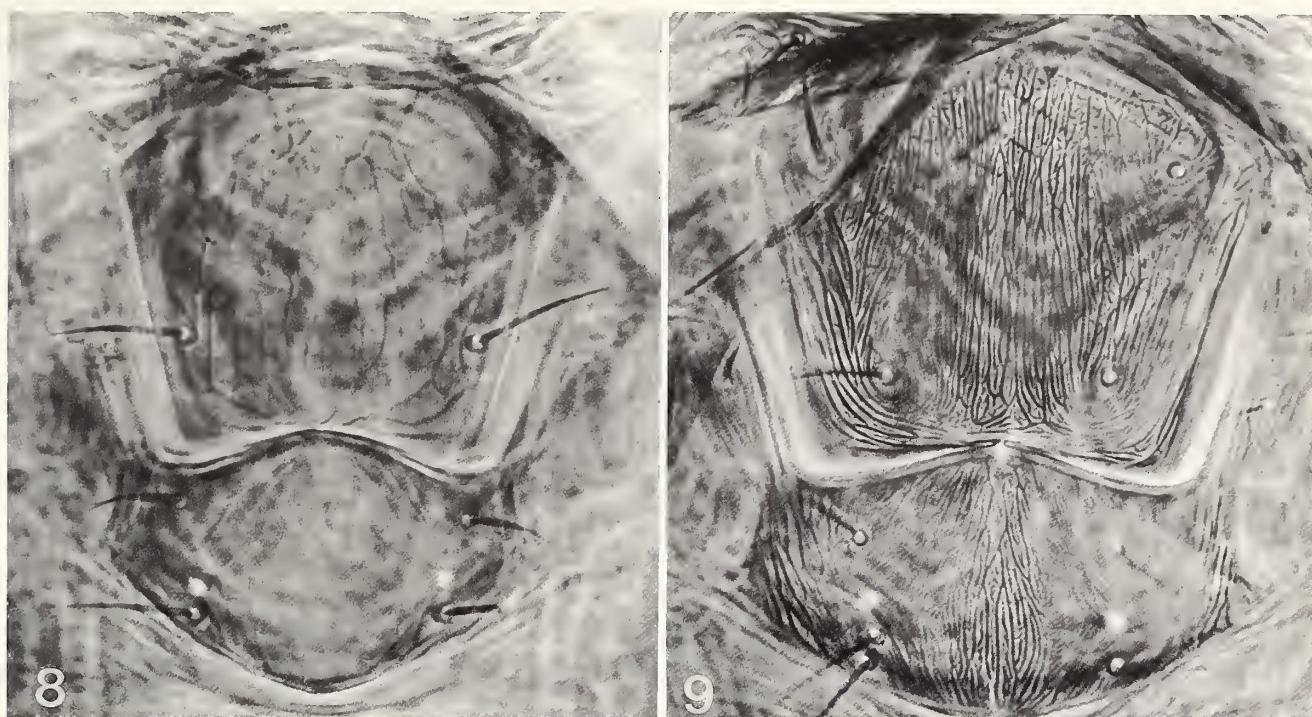
#### *Trichogramma lachesis*, new species

Figs. 1, 5, 7, 10–12

Description based on two males and one female, slide-mounted in Canada balsam. Unless referring to the unique female, quantitative data are means with an n of 2 or 3, as appropriate; range is reported if specimens differ considerably.

*Diagnosis.* *Trichogramma lachesis* is distinguished from other Lachesis Group species by the very broad ventral ridge (VR) and the absence of an intervolsellar process (IVP) (Fig. 11).

*Description.* Color light yellow brown; 0.47 mm in length; HTL = 0.12–0.13 mm (males), 0.14 mm (female). Maxillary palp with segment II short, obsolescent (Fig. 5). Forewing broad, 0.20 mm; FWW/FWL = 0.57; longest fringe setae 0.16 FWW; relatively few setae between major vein tracks, 8–13 between 4th and 5th tracks. Hindwing without anterior or posterior tracks, but two small, widely spaced setae



Figs. 8-9. Thoracic microsculpturing in the Lachesis Group of *Trichogramma*. 8. *Trichogramma atropos*. 9. *Trichogramma clotho*.

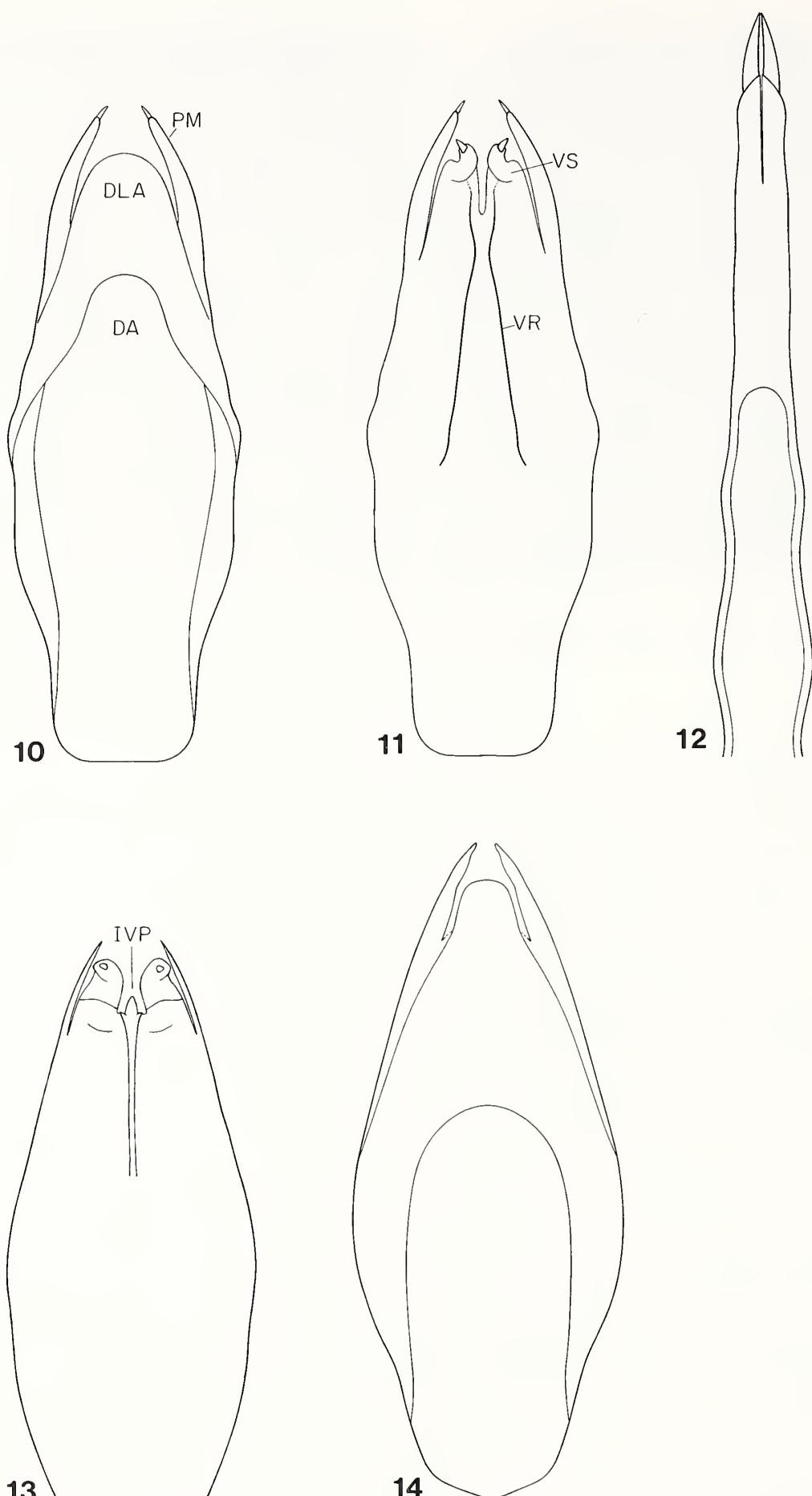
slightly posterior to basal half of middle track may represent posterior track setae. Mesoscutum and scutellum smooth, microsculpturing indistinct; scutellum with anterior pair of setae elongate, stout, ca. 0.6 length of posterior pair.

**Male.** Antenna (Fig. 1) with funicle 0.70 length of club, subequal to length of scape; F1 subquadrate, apical socket acentrally positioned; F2 1.6 as long as wide, 1.3 as long as F1, asymmetrically tapered from middle to relatively narrow apex, only slightly narrower than F1 at basal half; length of club segments 12:14:11, respectively; C2 slightly wider than C1; C3 narrower, subconical; longest setae on flagellum 2.3–2.7 width of F1; BCPS large, bulbous, formula 2-2-2-1-1; PS extending considerably beyond apex of segments, conspicuously so on C3, formula 0-0-1-1-2.

Genital capsule (Figs. 10, 11) 0.37 as wide as long, tapering moderately from widest point to apex; PM evenly curved, convergent to apex, appendiculate at apex; AD short, only 0.16 GL; DA large, its length 0.72 GL; DLA not lobed or notched at base, extremely broad its entire length, width of posterior extension subequal to that across parameres, broadly arcuate at apex, extending to apical  $\frac{2}{5}$  of AD; VS abruptly produced ventromedially at apical half, very narrowly separated from one another, extending slightly beyond apex of DLA, occupying ca. 0.7 AD; IVP absent; IB narrow; VR conspicuous, extremely broad, elongate, occupying ca.  $\frac{1}{2}$  BD; VP not visible. Aedeagus length (Fig. 12) 1.10 GL, 0.90 HTL; apodemes 0.51 AL; aedeagus widest at apodemes.

**Female.** Antenna with F1 and F2 subquadrate, about as broad as long, each with 1 BCPS on dorsal surface; club length subequal to length of scape, with two BCPS on dorsal surface (at basal and apical  $\frac{1}{4}$ , respectively) and five PS. Ovipositor moderately long, OL/HTL = 1.12.

**Types.** Male holotype. COSTA RICA. Guanacaste: Santa Rosa National Park, "Hacienda 3-0"; v-24/vi-14-1986. Allotype female, same data as holotype. Paratype



Figs. 10–14. Male genitalia in the Lachesis Group of *Trichogramma*. 10. *Trichogramma lachesis*, genital capsule (dorsal) (VS partially visible in dorsal view but not shown). 11. *Trichogramma lachesis*, genital capsule (ventral). 12. *Trichogramma lachesis*, aedeagus (ventral),

male, same data as holotype except "Hacienda 2-C"; i-31/ii-21-1987. The types are deposited as follows: holotype and allotype—United States National Museum; paratype—University of California, Riverside.

Santa Rosa is the former name of Guanacaste National Park. According to information received from Ian Gauld and Paul Hanson (in litt.) the types were collected in two different Malaise traps (one in shade, the other in a clearing) placed on the plateau (250–300 m) immediately west of park headquarters in young scrubby woodland.

*Notes.* The female allotype was collected with the holotype. Their association is based on correspondence of all comparable characters including color, structure of the maxillary palp, scutellar setal length, thoracic sculpturing, and hindwing setation.

**Trichogramma clotho, new species**

Figs. 2, 6, 9, 13

Description based on the unique male holotype (slide-mounted in balsam).

*Diagnosis.* *Trichogramma clotho* is distinguished from other Lachesis Group species by the distinctive rugulose microsculpturing on the thorax (Fig. 9), and the more elongate and apically tapered second funicular segment (Fig. 2).

*Description.* Color dark brown; 0.55 mm in length; HTL = 0.14 mm. Forewing broad, 0.23 mm in width; FWW/FWL = 0.57; longest fringe setae 0.15 maximum wing width; setation on disk similar to *lachesis*, 5 setae between 4th and 5th tracks, RS<sub>1</sub> consisting of only 2 setae. Maxillary palp (Fig. 6) with segment II longer, more distinct than in *lachesis*. Hindwing without anterior and posterior tracks. Mesoscutum and scutellum with distinct, rugulose microsculpturing (Fig. 9); scutellum with anterior pair of setae elongate, stout, ca. 0.6 length of posterior pair (type has a supernumerary posterior seta on left side).

Antenna with funicle 0.70 length of club and subequal to length of scape; F1 subrectangular, 0.8 as long as wide, apical socket acentrically positioned; F2 elongate, considerably narrower and longer than F1 (Fig. 2), strongly asymmetrically tapered from basal  $\frac{1}{3}$  to apex, 2.3 as long as wide, 1.9 as long as F1; length of club segments 14:14:18, respectively; C2 slightly wider than C1, C3 apparently considerably narrower and linear (partially collapsed in type); longest setae on flagellum 3.0 width of F1; BCPS shape and formula as in *lachesis*; PS extending considerably beyond apex of segments, formula 0-0-0-1-2.

Genital capsule (Fig. 13) 0.45 as wide as long; AD short, 0.15 GL; PM straight, narrow, convergent, apparently not appendiculate; DA large, its length 0.69 GL; DLA as in *lachesis*, extending 0.4 length of AD; VS slightly less strongly produced ventromedially than in *lachesis*, occupying ca. 0.8 AD; IVP present, moderately long, robust, subtriangular, extending 0.3 AD; IB wider, slightly greater than basal width of IVP; VR narrow, occupying 0.3 BD; VP short, slightly protuberant, at base of



showing bilobed structure and elongate phallotreme at apex. 13. *Trichogramma clotho*, genital capsule (ventral). 14. *Trichogramma atropos*, genital capsule (dorsal) (VS partially visible in dorsal view but not shown). DA = dorsal aperature of phallobase; DLA = dorsal lamina; IVP = intervolsellar process; PM = parameres; VR = ventral ridge; VS = volsellar digit.

IVP. Aedeagus length 1.21 GL; AL/HTL = 0.79; apodemes occupying 0.49 AL, aedeagus not wider at apodemes.

*Female.* Unknown.

*Type.* Holotype male. COSTA RICA. *Puntarenas:* Golfo Dulce, 13 km S Rincon, 10 m elev.; ii/iii-1989; Malaise trap; P. Hanson coll. Deposited in the United States National Museum.

**Trichogramma atropos, new species**

Figs. 3, 8, 14

Description based on the unique male holotype, slide-mounted in Canada balsam.

*Diagnosis.* *Trichogramma atropos* is distinguished from other Lachesis Group species by the subquadrate second funicular segment (Fig. 3), the presence of an incomplete anterior vein track in the hindwing, and the triangular posterior extension of the dorsal lamina (DLA) (Fig. 14).

*Description.* Color yellow brown; 0.48 mm in length; HTL = 0.15 mm. Maxillary palp II as in *lachesis*. Forewing broad, 0.20 mm in width, FWW/FWL = 0.54; longest fringe setae 0.19 wing width; disk moderately densely setate, with 7 linearly arranged setae between 4th and 5th tracks. Hindwing with anterior track of 3 setae; posterior track absent. Mesoscutum and scutellum smooth, microsculpturing indistinct; scutellum with anterior pair of setae elongate, stout, ca. 0.7 length of posterior pair (Fig. 8).

Antenna with funicle 0.70 length of club, subequal to length of scape; F1 subquadrate; F2 (Fig. 3) 1.2 as long as wide, 1.2 as long as F1, asymmetrically tapered only at apex of segment; length of club segments 12:12:11, respectively; C2 slightly wider than C1; C3 considerably narrower, subconical; flagellar setae relatively short and stout, abruptly tapered at apex, longest setae 1.8 width of F1; BCPS large, bulbous, formula 2-2-2-2-1; PS formula 0-0-0-1-2.

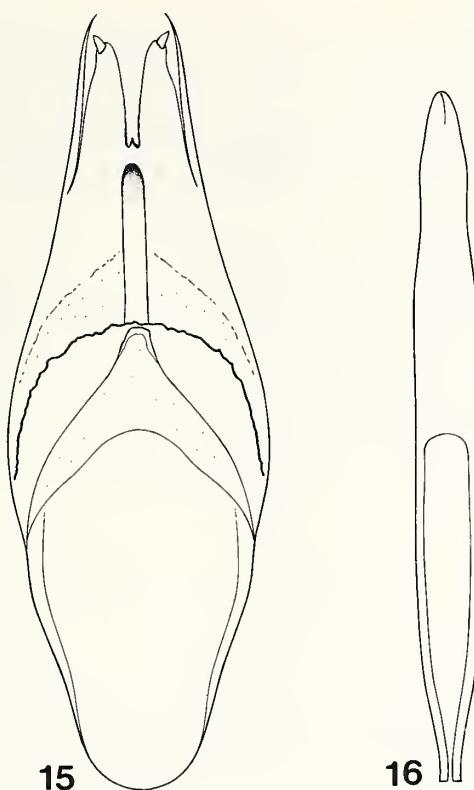
Genital capsule (Fig. 14) 0.43 as wide as long, gradually tapering from widest aspect to apex; PM relatively straight, evenly convergent to apex, apparently not appendiculate; AD 0.27 GL; DA relatively narrow, its length 0.58 GL; DLA not obviously notched or lobed at base, its posterior extension broadly subtriangular, tapering evenly from base to bluntly rounded apex, extending to apex of VS; VS asymmetrically narrowed apically, produced ventromedially, occupying 0.70 AD; IVP present but inconspicuous, short, linear, occupying only 0.1 AD; IB narrow; VR difficult to discern in type, apparently narrow and relatively short; VP not protuberant, positioned considerably basal to IVP. Aedeagus length 1.11 GL, 0.70 HTL, apodemes 0.41 AL; aedeagus not wider at apodemes.

*Female.* Unknown.

*Type.* Holotype male. VENEZUELA. *Merida:* La Montaña Station, 2,435 m elev.; iv-3/13-1988; Malaise trap; A. T. Finnimore & C. E. Baxfield, collrs. Type deposited in United States National Museum.

**PRIMAEVUM GROUP**

As in the Lachesis Group except as follows: F1 of male antenna with a linear PS. Aedeagus not bilobed, phallotreme restricted to apex. Hindwing with an incomplete but distinct posterior vein track.



Figs. 15–16. Male genitalia in the Primaevum Group of *Trichogramma*. 15. *Trichogramma primaevum*, genital capsule (dorsal). 16. *Trichogramma primaevum*, aedeagus (ventral).

*Notes.* This group includes a single species from Queensland, Australia. The female is unknown. Male antennal segmentation, maxillary palp structure, and marginal vein setation are as in the Lachesis Group. Aedeagus structure, however, is as in all other *Trichogramma*.

#### *Trichogramma primaevum*, new species

Figs. 4, 15, 16

Description based on the unique male holotype, slide mounted in Canada balsam.

*Diagnosis.* *Trichogramma primaevum* is distinguished from members of the Lachesis Group by the simple aedeagus and its shorter phallotreme (Fig. 16), and by the presence of a placoid sensillum (PS) on the second funicular segment of males. The segmented male club separates the species from all other congeners.

*Description.* Color yellow brown, legs and abdomen lighter than rest of body; 0.60 mm in length; HTL = 0.15 mm. Maxillary palp with a short second segment. Forewing broad, 0.26 mm wide; FWW/FWL = 0.60; stigmal vein relatively short, robust, with a slightly constricted neck; fringe unusually short, longest setae only 0.06 FWW; 18 setae between 4th and 5th tracks. Hindwing with posterior track of 5 setae extending 0.45 distance from hamuli to apex; anterior track complete to apex. Mesoscutum and scutellum relatively smooth, microsculpturing indistinct; scutellum with posterior pair of setae short (0.016 mm long), only ca. half the length of those in congeners; anterior setae slightly shorter.

Antenna (Fig. 4) with funicle 0.58 length of club, 0.73 length of scape; scape somewhat broader than in congeners; F1 subquadrate, apical socket not acentrally positioned; F2 1.4 as long as wide, 1.4 as long as F1, asymmetrically tapered at apex;

Table 1. Characters distinguishing species of the Lachesis and Primaevum groups of *Trichogramma*.

Characters <sup>1,2</sup>	Species			
	<i>lachesis</i>	<i>clotho</i>	<i>atropos</i>	<i>primaevum</i>
1.	0	1	0	0
2.	0	0	0	1
3.	0	0	1	2
4.	1	2	0	0
5.	0	1	0	0
6.	0	0	0	1
7.	1	1	1	0
8.	1	1	1	0
9.	1	0	0	0
10.	0	0	1	2
11.	0	2	1	1
12.	1	0	0	0
13.	1	1	1	0

<sup>1</sup> Characters: 1. Dorsum of thorax smooth, with indistinct microsculpturing (0) (Fig. 8); with distinct, rugulose microsculpturing (1) (Fig. 9). 2. Hindwing with posterior vein track absent (0), present (1). 3. Hindwing with anterior vein track absent (0), incomplete (1), complete to apex (2). 4. F2 of male antenna slightly (0) (Fig. 3), moderately (1) (Fig. 1), strongly (2) (Fig. 2), tapered to apex. 5. Length of F2 of male antenna less than 1.5 (0) (Fig. 1), or almost 2.0 (1) (Fig. 2), that of F1. 6. F2 of male antenna without (0) (Fig. 1), or with (1), a PS (Fig. 4). 7. AL shorter (0) (Figs. 15, 16), or longer (1) (Figs. 11, 12), than GC. 8. Aedeagus not bilobed at apex, phallotreme restricted to apex (0) (Fig. 16); aedeagus bilobed apically, phallotreme more extensive, extending from apex onto ventral surface (1) (Fig. 12). 9. PM appendiculate apically (1) (Fig. 10), or not (0) (Fig. 13). 10. Posterior extension of DLA broad, ligulate (0) (Fig. 10); broad, triangular (1) (Fig. 14); extremely narrow, filiform (2) (Fig. 15). 11. IVP absent (0) (Fig. 11), minute (1) (Fig. 15), well developed (2) (Fig. 13). 12. VR narrow (0) (Fig. 13), very broad (1) (Fig. 11). 13. VS relatively straight, unmodified (0) (Fig. 15); contorted, produced ventromedially (1) (Figs. 11, 13).

<sup>2</sup> Character codes are ordered phenetically.

maximum length of club segments subequal; C1, C2 subequal in width, C3 considerably narrower, subconical; flagellar setae relatively short and stout, abruptly tapered at apex, longest setae 1.67 width of F1; BCPS relatively small, subglobose, difficult to discern in type, formula apparently 1-2-2-1-1; PS formula 0-1-1-1-2.

Hind tibia atypical for genus, broadly notched dorsoapically.

Genital capsule (Fig. 15) 0.34 as wide as long, strongly, evenly tapered from widest point to apex and to base; PM narrow, slightly curved at apex only, not appendiculate; AD 0.17 GL; DA smaller than in Lachesis Group, its length 0.45 GL; DLA unique: base of structure consists of a broadly and lightly sclerotized area intermediate to a basal and an apical membranous region, basal membranous area subtriangular and well defined, apical area poorly differentiated; posterior extension of DLA uniformly very narrow, subfiliform, curving ventrally, extending from apex of subtriangular membranous area to near base of volsellae; DLA not notched or lobed at base; VS straight elongate, narrowly separated, occupying ca. 0.90 AD; IVP minute, subtriangular; IB narrow, no broader than basal width of IVP; VR narrow, elongate, occupying 0.43 BD; VP not protuberant, extremely basal in position, near midpoint of VR. Aedeagus length (Fig. 16) 0.93 GL, 0.82 HTL; apodemes 0.47 AL.

*Female.* Unknown.

*Type.* Holotype male. AUSTRALIA. *Queensland:* Westwood, 9.6 km NE, on Hwy. 66 at Valentine Creek; iv-12-1988; screen sweeping; G. Gordh & J. D. Pinto, collrs. Type deposited in the Queensland Museum, Brisbane, Australia.

*Etymology.* The specific name *primaevum* is a Latin word for young or early (primeval).

*Notes.* *T. primaevum* is similar to species of the Lachesis Group only in antennal segmentation, the two-segmented maxillary palp and the presence of a submarginal seta on the marginal vein. Hindwing setation, aedeagus and genital capsule structure, scutellar setal length, and the PS formula on the antenna all differ.

The PS on F2 of the type's left antenna is oriented longitudinally as is normal in Trichogrammatidae; its counterpart on the right antenna is oriented transversely.

#### DIAGNOSES AND SPECIES RELATIONSHIPS

The four new species share characters absent in all other *Trichogramma*. The male antenna has both the funicular and club segments unjoined, the maxillary palp is two-segmented, and the marginal vein has a seta distinctly behind its anterior border. Species differences are summarized in Table 1. *Trichogramma primaevum* is clearly differentiated from the Lachesis Group. Its relationship to this group and other components of the genus cannot yet be resolved. The phenetically similar species of the Lachesis Group are tied by aedeagal structure and hindwing setation. Species relationships within the group also are questionable. The more highly modified F1 in *lachesis* and *clotho* suggests that they are more closely related than either is to *atropos*. The occurrence of an IVP in *clotho* and *atropos*, and not in *lachesis* is in contradiction, but only if the absence of the IVP is plesiomorphic. The distinctive thoracic microsculpturing in *T. clotho* separates it from related species and all other congeners (cf. Figs. 8, 9).

#### DISCUSSION

*Trichogramma* currently is divided into two subgenera, the nominate subgenus and *Trichogrammanza*. *Trichogrammanza* was described by Carver (1978) based on male antennal segmentation (two distinct funicular segments, single club segment). It includes three Australian species and was recently reviewed by Oatman and Pinto (1987). The nominate subgenus, world-wide in distribution and with over 160 named species, is divided into a variable number of species groups depending on authority (Nagarkatti and Nagaraja, 1977; Voegeli and Pintureau, 1982; Viggiani and Laudonia, 1989).

The differences between the species of the Lachesis and Primaevum groups, and congeners are of a greater magnitude than between the nominate subgenus and *Trichogrammanza*, and would also justify subgeneric, perhaps even generic, treatment on phenetic grounds. Thus, the placement of these new taxa within the nominate subgenus is somewhat discordant to the current classification.

This conservative approach is proposed until a better understanding of phylogenetic relationships in the genus is gained. Phylogenetic questions concern the relationship of *Trichogrammanza* to the nominate subgenus, and the relationship of the Lachesis and Primaevum groups to one another and to congeners.

With regard to *Trichogrammanza*, male antennal segmentation prompted Nagaratti and Nagaraja (1977) to consider the taxon intermediate to *Trichogrammatoidea* and *Trichogramma* (*Trichogramma*). However there is reason to suggest that, rather than representing the sister taxon of the nominate subgenus, *Trichogrammanza* is of more recent origin, and is actually derived from an ancestor with complete antennal ankylosis in males. The presence of rare males with typical *Trichogramma* (*Trichogramma*) antennae (completely fused flagellar segments) in an isofemale-derived laboratory culture of *T. (Trichogrammanza) funiculatum* Carver (unpubl. data), suggests that the unjoined funicular segments may not be plesiomorphic, but a reversal instead. Also, the male genitalia of the three species of *Trichogrammanza* are not distinctive in any way but instead are similar to those of the Palearctic *T. (Trichogramma) principium* Sugonjaev and Sorokina, and relatives (Oatman and Pinto, 1987). The possibility that the latter assemblage represents the sister taxon of *Trichogrammanza* warrants investigation. Of course, subgeneric treatment for *Trichogrammanza* could not be supported on cladistic grounds if such a relationship to this or any other component of the nominate subgenus is shown.

In my opinion the Lachesis and Primaevum groups do represent primitive lineages, basal to all other *Trichogramma*. This is suggested by male antennal structure which is remarkably similar to that in other genera of Trichogrammatini, namely *Australufens* and *Trichogrammatomyia* (cf. figs. 1 and 4 with figs. 3D & 57B in Doutt and Viggiani, 1968), and by the two-segmented maxillary palp. Because these similarities presumably are plesiomorphic they do not argue for the Lachesis and Primaevum groups representing a single lineage. The bilobed aedeagus and its elongate apicoventral phallotreme in the Lachesis Group are unique and perhaps justify isolation at the subgeneric level. The former trait probably is derived. The ventral extension of the phallotreme, however, was considered primitive in Hymenoptera by Snodgrass (1941, 1957). A detailed comparison of aedeagal structure in *Trichogramma* is required before a more definitive estimate of polarity of these characters can be given. Unfortunately, the paucity of Lachesis Group specimens prevents this. In any case, formal treatment of the Lachesis Group would still leave the position of *T. primaevum* unsettled. Although placing both groups in the nominate subgenus is not entirely satisfactory, it seems preferable to erecting one or two inadequately supported subgenera.

#### ACKNOWLEDGMENTS

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## NOTES AND COMMENTS

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### OBSERVATIONS ON THE BIZARRE JELLY MASS HABIT OF LARVAL *GERANOMYIA* (DIPTERA: TIPULIDAE: LIMONIINAE)

An unusual specimen of a larval *Geranomyia* tipulid was found at the Finca La Selva Biological Station in Heredia, Costa Rica, on 8 February, 1989. It was found while examining leaves among trees in the old coffee finca on the station property. Suspended beneath one leaf, at about 6 feet from the ground, was a globular mass about 2.5 cm in diameter, made of a clear jelly-like substance and harboring a verdent green larva (Fig. 1). The larva was obviously a mature instar nematoceran, with an evident head capsule and thickened thoracic region. Posterior spiracles barely penetrated the surface of the jelly mass, no doubt allowing the larva to respire. When disturbed, the larva rolled around in the jelly mass, even retracting the posterior spiracles. With sunlight coming through the leaf the green larva became almost invisible. It is unknown as to what the larva may have been feeding upon, how it found its way to such an inaccessible spot, and whether or not the jelly is a feature of the last (fourth) instar. The specimen, with leaf, was placed in a moist petri dish and 4 days later it emerged as a female *Geranomyia*, with intricately patterned wings typical of the genus. Being such an unusual habit for any fly, this prompted us to describe the habit and morphological modifications that the larva might have for this peculiar existence. Other references to the jelly mass habit of larval *Geranomyia* are reviewed, and possible origins of the habit are given.

The larval exuvium (with head capsule) was originally pointed on the same pin as the adult specimen, but it was then softened in KOH and slide mounted for compound microscopy. Specimens are in the AMNH. Dorsal and ventral views of the head capsule are shown in Figures 2 and 3, respectively. The rest of the larva was not examined, since the exuvium was not well preserved. The larva has a typical limoniine head capsule (Hennig, 1950), with broad lateral plates which are fused to the fronto-clypeus dorsally forming a blackened, strongly sclerotized area along much of its length (ventrally the lateral plates are connected only anteriorly to form the mentum). The antennae are 2-segmented, inserted above the base of the mandibles (the typical, terminal papilla may have been lost during molting). The mandible is of the cutting-chewing type, strongly sclerotized, and with one pointed tooth at the apex and five smaller teeth along the inner margin. The maxilla possesses a sclerotized cardo and stipes (the lacinia not being well defined). Eight visible pointed teeth occur ventrally on the hypopharynx (the number dorsally was not visible). The mentum possesses 11 rather blunt teeth, the median one largest and slightly elevated. Features of the head capsule do not differ significantly with other limoniines (cf. *Geranomyia canadensis* [Alexander and Malloch, 1920], see Cramer, 1969), indicating that the diet may not be so unusual as to require distinct morphological specialization. No evidence of folivory was evident. Such a habit is very rare in tipulids, and occurs, for example, in *Limonia* (*Dicranomyia*) *kauaiensis*, which mines leaves of *Crytandra* in

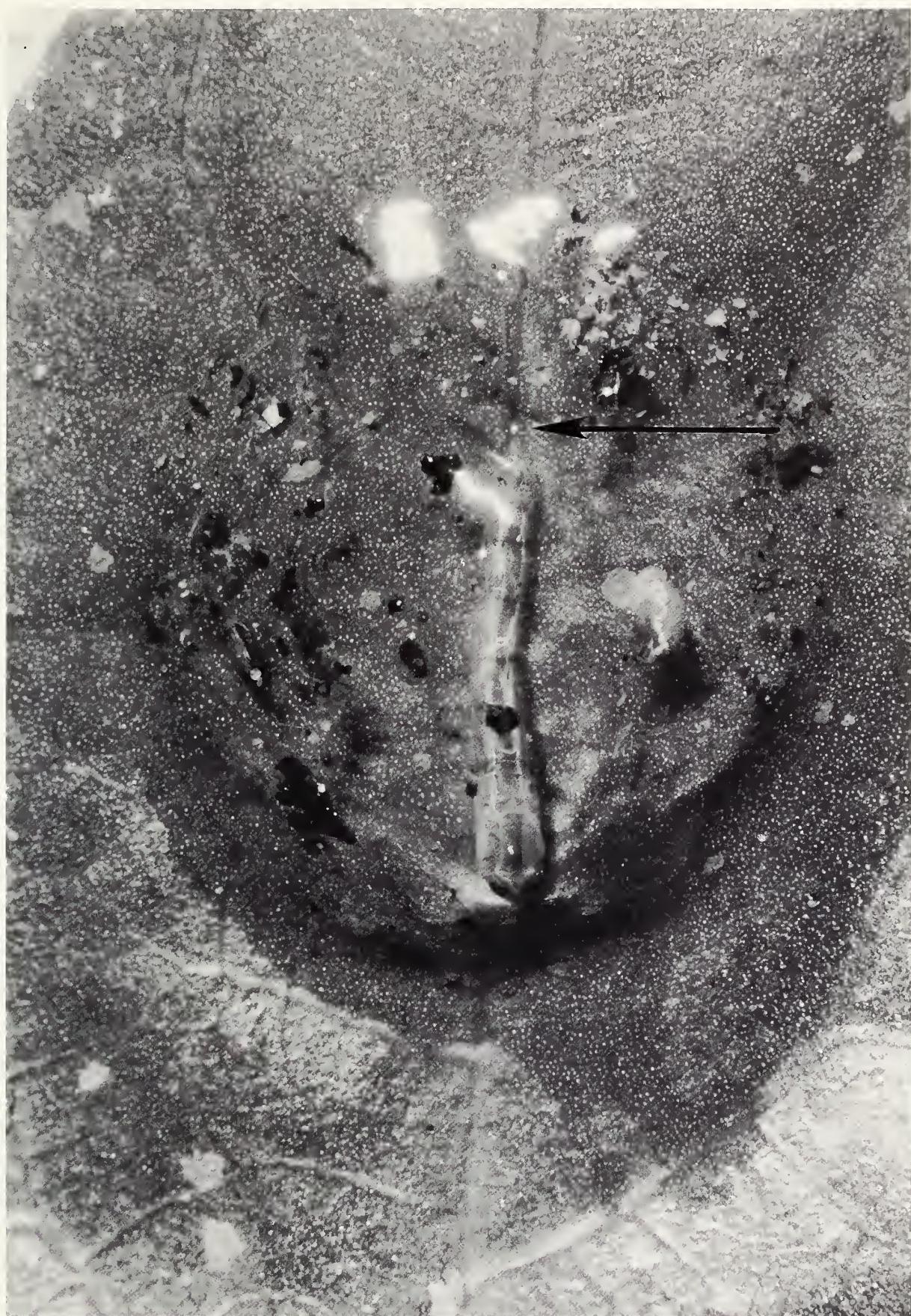
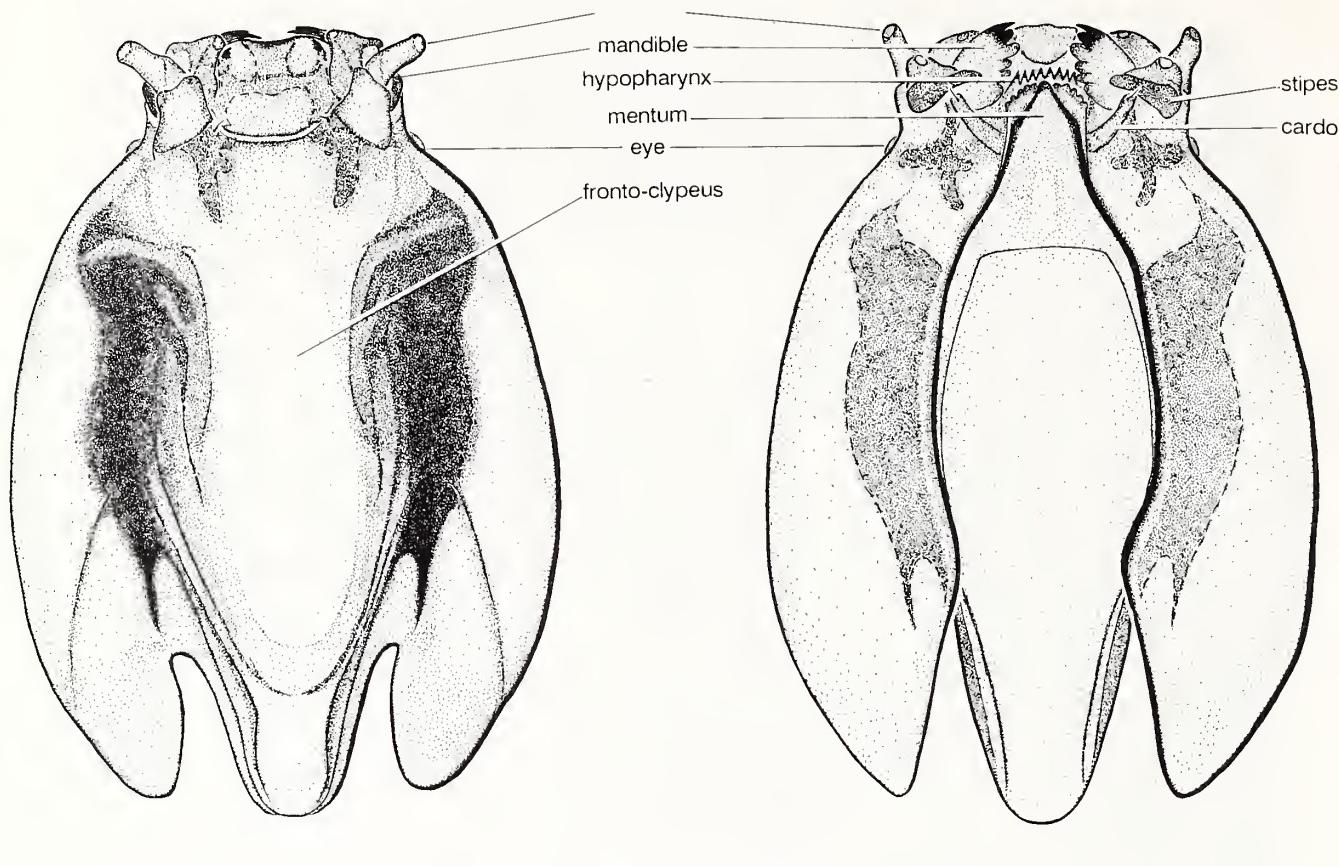


Fig. 1. Photograph of *Geranomyia* sp. fourth instar/prepupal larva in situ in jelly mass under leaf. Arrow points to posterior spiracle opening.



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3

Figs. 2, 3. Head capsule from larval exuvium of Costa Rican *Geranomyia* female. 2. Dorsal view. 3. Ventral view.

Hawaii (Swezey, 1915). The *Geranomyia* specimen might have been grazing upon an algal film on the leaves.

The bizarre jelly mass habit of tipulids has actually been reported elsewhere, by Hingston (1932) for a specimen in British Guiana. So far, this habit is known only in *Geranomyia*. Hingston reported (p. 342): ". . . in the forest there was a crane-fly, *Geranomyia*, which suspended its pupa in a globule of jelly wrapped around the tip of Turu palm leaf. The globule was a firm gelatinous substance, rather smaller than a hazel-nut and clear as water. Indeed, its appearance was that of a large drop of water about to fall from the end of the palm leaf. . . . The pupa was clearly visible inside it. It rested in a nearly vertical position, its head upward in the broad part of the globule, its tail below and close to the leaf. Its colour was grass green with five dark bands that half-crossed its body." The Costa Rican specimen was not found in a pendulous jelly mass the way Hingston reported (the larva in fact was parallel to the leaf surface), nor were there obvious dark bands across the body. Hingston's specimen, with others, were later described as *Limonia (Geranomyia) gelatifex* (Edwards, 1934). Alexander and Alexander (1970) indicate *G. gelatifex* to be a junior synonym of *Limonia (G.) recondita* (Alexander), 1921. They report the distribution of *recondita* to be from Guyana and Brazil to Ecuador, Peru, and Panama. The species identity of the Costa Rican female could not be determined with certainty since tipulid species are generally defined on the basis of male genitalia.

It is evident that the jelly mass is produced directly from the larva. There is no evidence that leaves exude the substance, nor even that the larva sequesters the

substance from the plant. In fact, a similar jelly substance is produced in much smaller quantities by *Limonia triocellata*. This is a broadly mycophagous species breeding in various macrofungi in the eastern United States. As the mature larvae become pharate pupae, they form mucilaginous tunnels in the fungal context or substrate below, in which they pupate. Production of the jelly substance may, in fact, be widespread in limoniines and just produced in overabundance by *Geranomyia*. *Geranomyia* pupating on such exposed surfaces as leaves would probably be highly susceptible to hymenopterous parasitoids, and the jelly mass may afford at least some concealment or physical barrier.—David Grimaldi, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192; and Chen Young, Section of Invertebrate Zoology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213.

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## BOOK REVIEW

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**Women in the Field, America's Pioneering Women Naturalists.**—M. M. Bonta. 1991.  
Texas A&M Press, College Station, TX. \$13.95.

Marcia Myers Bonta's *Women in the Field* is a must read for men and women naturalists, botanists, ornithologists, ecologists, entomologists and historians. It is written in a style that is enjoyable for light bedtime reading; yet provides rigorous historical information rendering it a valuable reference book. Chapters are dedicated to 25 women who, in the author's estimation, made the most important contributions to their field, and about whom adequate information could be obtained. They are grouped in 6 sections: I. The pioneers, II. The naturalists, III. The botanists, IV. The entomologists, V. The ornithologists, and VI. The ecologists. Each section contains a preface that highlights the accomplishments of several other women who either had less impact or whose lives were less well documented. The book is illustrated with 30 photographs of the women in their element or their artwork. Reference material is not included in the text, but a selected bibliography is provided at the end for readers who wish to obtain source material used by the author. The book also includes an index. Each chapter stands alone, such that readers can selectively learn about the careers of specific women. However, the author often points out connections between these women, since many of them were acquainted with each other.

It is remarkable how many women naturalists emerged "in the days when women were perceived as fragile beings fit only to keep house and raise children." Here I describe some of my favorite chapters to give readers the flavor of Bonta's writing style. Martha Maxwell was a mid 19th century intrepid Colorado huntress and taxidermist who is pictured with a gaudy display of stuffed deer, elk and bighorn sheep at the Philadelphia Centennial. She often went camping alone in the mountains and also had a passion for wildflowers. Mary Treat, a late 19th century naturalist of the New Jersey Pine Barrens, spent many productive hours in her backyard surrounded with an arbor vitae hedge 15 feet high and 150 feet in circumference, which became known as her "insect menagerie" or "arachnidian menagerie." Annie Montague Alexander, a late 19th century quintessential naturalist and daring explorer, preferred to sleep outside in the desert "where half the universe shown down upon us, not a tree to break the wonderful arch of the Milky Way reaching from horizon to horizon." Alice Eastwood, best known for her early 20th century botanical contribution to the western US flora, was completely self-taught, raised mostly by relatives and foster parents after her mother died when Alice was 6. At age 91, she was made honorary president of the International Botanical Congress in Sweden where she sat in the chair of Linneaus. Ann Haven Morgan was trained as an aquatic ecologist and mayfly expert by J. G. Needham at Cornell University in the early 20th century. She was once described as "a gray-haired lady knee-deep in muck and water ferociously pursuing nasty little herbivora and carnivora with a net" never wanting to "come out of some particularly oozy mudhole." I personally aspire to be described similarly when my hair becomes more gray than brown.

The last chapter describes the inspiring career of Rachel Carson, who was labeled by some critics as a "mere birdwatcher," due to the fact that she was much too qualified a scientist to treat as a "hysterical woman" for publishing *Silent Spring*, one of the most influential and controversial conservation works of all time. Unlike many of her predecessors who had enjoyed long and healthy lives, Rachel Carson tragically died of cancer at the age of 56, "mourned throughout the world by those who love the earth."

The lives of three entomologists are described in detail. Annie Trumbull Slosson, known in the late 19th century as "the old bug woman" was often observed on the slopes (or summit) of Mt. Washington in New Hampshire with her "butterfly net." She also spent time collecting insects in Florida and in the Delaware Water Gap. She discovered many new insect species including Lepidoptera and Hymenoptera. After having a new moth species named after her, she remarked, "Without a thought of irreverence I felt like expressing my willingness to depart in peace now that I had seen this greatest of all earthly honors descend upon my humble head. An insect named for unworthy me! And the name so sonorous and delightful in sound. *Inguromorpha slossoni!* Like the proverbial Mesopotamia of the eloquent preacher it stirred one's soul and I think I murmured it even in my sleep." When that particular species was superseded, she lamented that it sunk "into the dread valley of synonymy."

Edith Patch, best known for her work on biology of aphids and also for her children's books on natural history, was one of the few women naturalists who was classically trained, graduating as an English major from the University of Minnesota in 1901, and eventually receiving a M.S. degree from the University of Maine and a Ph.D. from Cornell University under John Henry Comstock. She relentlessly pursued the study of entomology despite early warnings that entomology was not a suitable profession for a woman. She was given an early opportunity by Dr. Charles D. Woods, director of the Maine Agricultural Experimental Station who came under some criticism for hiring a woman. "When one of the leading Bureau of Entomology men remarked to Dr. Woods, 'I hear you have appointed a woman as entomologist. Why on earth did you do that? A woman can't catch grasshoppers,' he received the drawled reply, 'It will take a lively grasshopper to escape Miss Patch.' "

The chapter on Anna Botsford Comstock was touching and masterfully written. Working in the shadow of her husband, at the turn of the century she was appointed, and then unappointed as an assistant professor of nature study because the Board of Trustees at Cornell University objected to giving a woman professorial status. John Henry Comstock was highly supportive collaborating with Anna on numerous projects for which she not only did the artwork, but also some of the writing. In addition she amassed an impressive list of scholarly achievements of her own. The most famous was her *Handbook of Nature Study*, which has affected the lives of many children. My personal favorite is *The Ways of the Six-footed*, a charming account of her own observations of insects. After many years of teaching and scholarship, she was eventually appointed as an assistant, then a full professor the same year that women finally received the vote in this country. She and her husband, childless, but not by choice, "adopted" a long line of children and graduate students for whom they provided not only emotional but also financial support. Tragically, John Henry Comstock suffered a stroke, after which Anna continued to work while caring for

him. Four years later she died of cancer two weeks after teaching her last class in her home in Ithaca. Liberty Hyde Bailey described her as an unfailing humanitarian who left "a fragrant memory of high achievement, noble service, unselfish cooperation, constructive counsel, inspired teaching, loving kindness and unforgettable companionship."

In the preface the author points out many attributes that these pioneer women naturalists had in common. One of them was modesty, as so aptly illustrated in the quote from Annie Trumbull Slosson. None liked typically "women things" like housework or clothes, although most of them did enjoy cooking for their friends. Some had been favorite daughters of enlightened fathers who appreciated nature themselves, and others had independent mothers as role models. Of the 25 women portrayed in this book, most of them never married or else started their careers after their husbands died. Six of them had supportive husbands while two were actively discouraged by their husbands. Only two ever had children. Most were self-taught and did not have professional positions. Some even turned over their materials to men professionals for publication in books and journals.

The author's hope was that "the lives and thoughts of my women naturalists will not only convince others that women and nature were and still are compatible, but also that the women's contributions to the study of nature were important—in fact amazing, given the prejudices they had to contend with." I found the book delightful, captivating and inspiring. I will encourage both my young son and daughter to read it some day to gain an appreciation of the relatively supportive environment within which their ecologist mother and hopefully they will we able to grow, in contrast to the harsh social climate that acted as a major hurdle during the 19th and much of the 20th centuries for women who were interested in pursuing the study of nature.—*Barbara L. Peckarsky, Department of Entomology, Cornell University, Ithaca, New York 14850-0999.*

## OBITUARY

IN MEMORIAM  
LAVERNE L. PECHUMAN  
1913–1992



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Dr. LaVerne L[eRoy]. Pechuman, or Verne to nearly everyone who knew him, Professor Emeritus of the Department of Entomology, Cornell University, and an international authority on the taxonomy of the blood-sucking flies of the family Tabanidae, died Monday, March 30, 1992, at Strong Memorial Hospital, Rochester, New York, after a short battle with cancer. He was 78 years old, and had continued to be active in his research until about three weeks before his death.

He was born October 18, 1913, in Lockport, New York, the son of Henry J. and Anna Brege Pechuman. He attended the Lockport public schools, and graduated from Lockport High School in 1930. After one year of post-graduate work, he matriculated at Cornell University, and graduated in 1935 with a bachelor's degree in Entomology. In July 1935, he was appointed an assistant in Entomology for the Dutch elm disease investigation being conducted jointly by the Departments of Entomology and Plant Pathology. He was admitted to the Graduate School at Cornell in September 1935. During the initial course of work on the Dutch elm disease, it was thought advisable to conduct a comprehensive survey of the various insects found associated with elm, and with special reference to their potential to transmit the causative organism of Dutch elm disease. Verne carried out these early biological investigations, first begun in 1934 by Drs. Philip A. Readio and Henry Dietrich, under the aforementioned professors' direction and later that of Dr. D. L. Collins. Pechuman's work culminated in a thesis entitled "Preliminary account of the insects found in the bark and wood of the American elm (*Ulmus americana* L.)," and in February 1937 he successfully completed requirements for a master's degree in Entomology. Verne's doctorate work was a continuation of his research on the Dutch elm disease, again under the able direction of Dr. Readio. A thesis entitled "The insects found in the bark and wood of the American elm (*Ulmus americana* L.)" was submitted to the Faculty of the Graduate School of Cornell for the degree of Doctor of Philosophy in June 1939.

Upon the completion of Verne's doctorate, he gained employment with the Ortho

Division of the Chevron Chemical Company (formerly California Chemical Co.). Beginning as a field representative (1939–45) in the company, he rose through the ranks, first from a Branch Manager (1945–47), to a District Manager (1947–61), and finally to a senior research scientist (1961–62). After nearly 25 years of dedicated service to Chevron Chemical Co., he returned to academia and Cornell University, joining the entomology faculty in 1962 as an associate professor and curator of the world famous insect collection. He was named full professor in 1972. Soon after his retirement in 1982, he was awarded the title of professor emeritus.

Among his academic peers and colleagues, Verne Pechuman will be best remembered as a world authority on the systematics, biology, and distribution of horse flies and deer flies (Tabanidae). During his 20 years as curator of the Cornell University Insect Collection, he is credited with amassing a collection of well in excess of 40,000 tabanid specimens, the largest and most geographically diverse assemblage of world Tabanidae in a North American university collection.

In the early 1970s, while collaborating with Dr. Mathias J. Kemen, Jr., a Cornell veterinarian, on the annoying biting and blood-sucking habits of horse and deer flies, and, in an attempt to answer the plight of New York dairymen and horse owners, Verne designed a mechanical trap (a prototype of which he used previously to make general collections of tabanids) to capture and significantly reduce the number of flies in a given area. It is a known fact that dairy cattle attacked by these biting flies often show a significant drop in milk production, and in horses these flies can be vectors of a debilitating viral disease known as equine infectious anemia. His broad-based knowledge of tabanid biology and especially of some of the behavior traits of these flies was the basis for the efficacy of this mechanical trap. Tabanid flies, which are attracted to dark, moving objects, are lured to the trap by a swinging, shiny, black ball, and a carbon dioxide supply (dry ice), which fools the flies into thinking there are live animals about (anthropomorphically speaking!). Once inside the trap, the flies move upward towards light and are captured and killed by an insecticide in the trap head. This trap design is still in general use today.

Although his primary taxonomic and biological work focused principally on the horse and deer flies, other interests of his included following the emergence of the various broods of the periodical cicada (the 17-year locust) in the eastern United States, a fascination with the effect of Pleistocene glaciation on several groups of insects, and yearnings in the history and prehistory of Upstate New York, local native American history, archaeology, and botany.

Verne loved the out-of-doors, and on many occasions he seized the opportunity to go collecting, usually to his favorite bogs around central New York to find the pesky horse and deer flies. He also had an admiration for plants, of which he knew many, if not most, of the local native and cultivated species. He had an inordinate fondness for trilliums, however—so much so that he authored several articles in the early 1960s. In *Science on the March*, a Buffalo Museum of Science publication, April and June 1962 issues, Verne reported on a multiplicity of forms of an uncertain status growing on the Tonawanda Indian Reservation in Genesee and Erie Counties. While living in western New York, he built up a significant collection of most of the North American species of *Trillium*, including some natural hybrids and a number of specimens of aberrations of some species. He also exchanged *Trillium* specimens with botanists in Japan, which are still known to be growing in his native Lockport.



Drs. Mathias J. Kemen, Jr. (left) and LaVerne L. Pechuman examine a mechanical trap, designed by Pechuman, that captures horse and deer flies.

In Spring of 1963 he donated specimens of his extensive collection, which included five Japanese species, to the Cornell Plantations.

Perhaps one of Verne's rarest tributes was his welcome as a guest at Tonawanda and Tuscarora Indian ceremonies. As well he was an adopted member of the Tonawanda Band (Hawk Clan) of the Seneca Indians. Through the years, Verne was always deeply concerned about the welfare of native Americans. On his many travels about New York State, he was known occasionally to detour to an Indian reservation to speak to and share times with his "adopted" brethren. In 1961, as a director and editor of The Niagara County Historical Society, Verne wrote an introduction to one of the early writings of David Cusick, a Tuscarora Indian: "Ancient History of the Six Nations," which was reprinted by the Society. In Verne's closing statement in

this introduction, he wrote "It is hoped that by reprinting this work of a Tuscarora Indian, it will be more readily available not only to students of anthropology but to anyone interested in a peculiar bit of Americana."

His numerous professional affiliations included the American Association for the Advancement of Science (AAAS), Entomological Society of America, Entomological Society of Ontario, American Entomological Society, New York Entomological Society (of which he was a long-time sustaining member), American Mosquito Control Association, Sociedade Brasileira de Entomologia, Buffalo Society of Natural Sciences, New York State Archaeological Association, and the Society for Pennsylvania Archaeology. As an active advocate for habitat preservation locally and globally, he belonged to The Nature Conservancy, Nature Sanctuary Society of Western New York, Bergen Swamp Preservation Society, and the Wilderness Society. He held advisory positions in many of these associations. Among his honors he was a member of Sigma Xi, appointed a fellow of AAAS in 1964 and a fellow of the Rochester Museum of Arts and Sciences in 1965, and listed in the *American Men of Science*. In 1960 he was made an honorary member of the Rochester Academy of Science, and also in that same year received a citation as "distinguished scientist" from the University of Buffalo.

Verne was author and coauthor of nearly 100 scientific papers and monographs (see "PUBLICATIONS . . ." below). He described 23 species (and subspecies) of horse and deer flies from around the globe as new to science (see "NEW TAXA . . ." below). Reflecting the respect that other entomologists had for his work, Verne had 26 species named after him as of 1986, mostly flies, but also species of other insect orders and a protozoan (see "TAXA NAMED . . ." below).

He is survived by a sister and brother-in-law, Dorothy and Benjamin Neal of San Jose, California; daughters and sons-in-law, Patricia and William Ferris of Bergen, New York, and Jean and James McIntyre of Waterville, Maine; grandchildren William and Michael Ferris; and one niece and several cousins. His wife of 52 years, Berta, preceeded him in death on December 3, 1991. Following a memorial service held in Ithaca, New York, he was buried in the family plot (Cold Springs Cemetery) in Lockport, New York, on April 4, 1992.

Professor Pechuman has left an enduring mark on the systematics of the Tabanidae to which he did much to fashion. As well he leaves behind a legacy of scholarship and dedicated service to Cornell University that includes not only his own publications but, also, his large collection of tabanid flies. The lives of his long-time colleagues and students are much richer today for having known and worked with him. We will remember him with fondness and great respect, and for his generosity of time, dash of good humor, and as an enthusiastic conversationalist and delightful companion. He will be dearly missed by his colleagues in the profession and by his many other friends.

#### NEW TAXA DESCRIBED BY L. L. PECHUMAN

1. *Silvius philipi* n. sp. 1938. USA: 10 mi. SE Lebanon, Oregon.
2. *Silvius quadrivittatus* (Say) var. *texanus* n. var. 1938. USA: College Station, Texas.
3. *Chrysops mutata* n. sp. 1939. MEXICO: Juan Manuel (near El Salto), Durango.
4. *Chrysops berta* n. sp. 1940. BRAZIL: Nova Teutonia, Santa Catharina.
5. *Chrysops striatula* n. sp. 1943. CHINA: Suifu, Szechuen.



Professor L. L. Pechuman, curator of the Cornell University Insect Collection from 1962–1982, examines one of the more than 12,000 drawers which house approximately 4–5 million insect specimens from around the world.

6. *Chrysops aenea* n. sp. 1940. CHINA: Yellow Dragon Gorge near Songpan, Szechuen.
7. *Glutops rossi* n. sp. 1945. CANADA: Port Haney, British Columbia.
8. *Catachlorops d'almeidai* n. sp. 1946. BRAZIL: Tingua, Rio de Janeiro.
9. *Chrysops atlantica* n. sp. 1949. USA: Rehoboth Beach, Delaware.
10. *Chrysops flavida celata* n. subsp. 1949. USA: Medford Lakes, New Jersey.
11. *Chrysops patricia* n. sp. 1953. PARAGUAY: Cerro Pelado.
12. *Chrysops argentina* n. sp. 1953. ARGENTINA: Tucumán.
13. *Tabanus dietrichi* n. sp. 1956. USA: Phelps Botanical Area, White Mountains, Arizona.
14. *Silvius pollinosus jeanae* n. subsp. 1960. USA: Naval Air Station, Corpus Christi, Texas.
15. *Hybomitra frosti* n. sp. 1960. CANADA: Orrville, Ontario.
16. *Tabanus wilsoni* n. sp. 1962. USA: Arkansas River, Arkansas Co., Arkansas.
17. *Pelecorhynchus penai* n. sp. 1967. CHILE: Pichinahuel, Arauco.
18. *Chrysops calvus* n. sp. (Pechuman & Teskey). 1967. USA: Allegany State Park, New York.
19. *Asaphomyia floridensis* n. sp. 1974. USA: Archbold Biological Station, Lake Placid, Highlands County, Florida.
20. *Chrysops dixianus* n. sp. 1974. USA: Wedge Plantation, McClellanville, South Carolina.
21. *Chrysops stonei* n. sp. 1977. JAPAN: Shirikishinai, Kamedagun, Hokkaido.
22. *Atylotus woodi* n. sp. 1981. CANADA: S. of Lot 31, Conc. Gore, Puslinch Twp., Wellington Co., Ontario.
23. *Apatolestes philipi* n. sp. 1986. USA: Dougout Wells, Big Bend National Park, Texas.

#### TAXA NAMED IN HONOR OF L. L. PECHUMAN

##### Protozoa-Eugregarinida

1. *Cometoides pechumani* Anderson & Magnarelli. 1978. J. Invert. Path. 31:324–328 (orig. descrip. p. 324). USA: Housatonic River, Milford, Connecticut.

##### Insecta

##### Odonata-Gomphidae

2. *Epigomphus pechumani* Belle. 1970. Studies on the fauna of Suriname and other Guyanas 11:1–158 (orig. descrip. p. 19). COLOMBIA: (no other data given).

##### Plecoptera-Capniidae

4. *Allocapnia pechumani* Ross & Ricker. 1964. Trans. Ill. State Acad. Sci. 57:88–93 (orig. descrip. p. 88). USA: Starkville, Herkimer County, New York, Otsquago Creek.

##### Homoptera-Aphididae

4. *Macrosiphum pechumani* MacGillivray. 1966. Can. J. Zool. 44:1085–1088 (orig. descrip. p. 1085). USA: Lockport, New York, ex *Smilacina racemosa*.

##### Diptera-Ceratopogonidae

5. *Culicoides pechumani* Cochrane. 1974. Florida Entomol. 57:125–135 (orig. descrip. p. 133). USA: Ringwood Game Preserve, Tompkins Co., New York.
6. *Forcipomyia (Euprojoannisia) pechumani* Bystrak & Wirth. 1978. U.S.D.A., Tech. Bull. no. 1591:51 pp. (orig. descrip. p. 34). USA: Cranberry Lake, St. Lawrence Co., New York.

### Diptera-Tabanidae

7. *Chrysops pechumani* Philip. 1941. Proc. Entomol. Soc. Wash. 43:113–130 (orig. descrip. p. 128). USA: Niles, Inyo Co., California.
8. *Amphichlorops pechumani* Barretto. 1948. Revista de Entomol. 19:401–417 (orig. descrip. p. 407). BRAZIL: “Faz. Serra, Itatiaia, Est. do Rio de Janeiro.”
9. *Cydistomyia pechumani* Philip. 1959. Fieldiana:Zool. 33:543–625 (orig. descrip. p. 557). PHILIPPINES: Negros Orientale, Mount Canlaon.
10. *Tabanus imitans* var. *pechumani* Philip. 1960. Florida Entomol. 43:171–174 (orig. descrip. p. 171). USA: “Gunntown,” Levy Co., Florida.
11. *Stenotabanus (Aegialomyia) pechumani* Philip. 1966. Ann. Entomol. Soc. Amer. 59:519–527 (orig. descrip. p. 522). MEXICO: 10 mi S. Telolutla, Vera Cruz.
12. *Dasybasis pechumani* Coscarón & Philip. 1967. Segundas jornadas entomoepidemiologicas argentinas 1 (1965):95–103 (orig. descrip. p. 97). CHILE: Tarapaca, Arica.
13. *Diachlorus pechumani* Fairchild. 1972. Florida Entomol. 55:219–229 (orig. descrip. p. 223). PERU: Quince Mil, Cuzco.
14. *Haematopota pechumani* Stone & Philip. 1974. U.S.D.A., Tech. Bull. no. 1489:240 pp. (orig. descrip. p. 159). LAOS: Vientiane Province, Ban Van Eue.
15. *Promycteromyia pechumani* Coscarón & Philip. 1979. Proc. Calif. Acad. Sci. 41:427–452 (orig. descrip. p. 436). CHILE: Aconcagua, Valle de Piuquenes.
16. *Hybomitra pechumani* Teskey & Thomas. 1979. Can. Entomol. 111:343–350 (orig. descrip. p. 346). CANADA: Alfred, Ontario.
17. *Esenbeckia pechumani* Wilkerson & Fairchild. 1983. J. Nat. Hist. 17:519–567 (orig. descrip. p. 549). PERU: Cuzco, Quincemil.

### Diptera-Otitidae

18. *Euxesta pechumani* Curran. 1938. Amer. Mus. Nov. no. 975:7 pp. (orig. descrip. p. 4). USA: Bronx, New York City, New York.

### Diptera-Sciomyzidae

19. *Dictya pechumani* Valley. 1977. Search Agric., N.Y. State Agric. Exp. Stn. (Ithaca), no. 7:44 pp. (orig. descrip. p. 4). USA: Ipswich, Massachusetts.

### Diptera-Chloropidae

20. *Elachiptera pechumani* Sabrosky. 1948. J. Wash. Acad. Sci. 38:365–382 (orig. descrip. p. 377). USA: 6 mi S of Middleport, New York, reared ex larvae from base of wild iris (*Iris versicolor*).

### Diptera-Agromyzidae

21. *Liriomyza pechumani* Spencer. 1986. U.S.D.A., Agric. Handb. no. 638:478 pp. (orig. descrip. p. 291). USA: Copeland, Collier Co., Florida.

### Diptera-Tachinidae

22. *Vibrissotheresia pechumani* Reinhard. 1943. Bull. Brooklyn Entomol. Soc. 38:78–90 (orig. descrip. p. 87). USA: Brewster, New York.

### Hymenoptera-Braconidae

23. *Opius pechumani* Fischer. 1970. Anz. öst. Akad. Wiss. Mathematische-Naturwissenschaftliche Klasse 107:12–32 (orig. descrip. p. 22). USA: near Portal, Arizona.

### Hymenoptera-Ichneumonidae

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James M. Carpenter, of the Department of Entomology, American Museum of Natural History, will assume the editorship of the Journal effective 1 November 1992. As of that date, all manuscripts should be submitted to him, using the conventions of the Instructions to Authors on the inside back cover.

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